The Causes and Consequences of Individual Variation in Survival and Fecundity of Great Lakes Piping Plovers (*Charadrius melodus*)

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Dedication

To YO:gX and all Great Lakes piping plovers—may you always remain part of the biodiversity of the Great Lakes coastal ecosystem

Abstract

The piping plover (*Charadrius melodus*) is a small shorebird endemic to North America and restricted to three breeding populations: Atlantic Coast, Great Plains, and Great Lakes. Listed as federally endangered in 1986, the Great Lakes population has numbered from 17 to 71 known breeding pairs. Despite recovery efforts, the population is far from the federal recovery goal of 150 breeding pairs. The purpose of my dissertation research is to understand the causes and consequences of individual variation in survival and fecundity during key breeding stages through four distinct methods of investigation: life-history theory, quantitative genetic analysis, population demography, and behavioral assessment. Effective conservation of small wildlife populations requires the intersection of many scientific disciplines and I seek to achieve this unification through the four chapters of my dissertation. First, I investigate how age and parental experience with breeding, a mate, and a nesting location influence reproductive success (Chapter 1). In chapter 2, I investigate the heritabilities of three fitness-related traits (chick body mass, natal dispersal distance, and female timing of breeding) to determine which are strongly environmentally-determined and thus susceptible to impacts of global climate change. In chapter 3, I tease apart the relative influences of various developmental and environmental factors at pre-fledging, post-fledging, and adult stages to more precisely inform population recovery actions. In my final chapter, I test the hypothesis that captive-reared chicks have lower survival rates than those reared in the wild because of a lack of threat recognition. The insights gained from my research not only pertain to this small shorebird breeding in the Great Lakes, but also provide a more comprehensive framework for analyzing data on marked individuals with the goal of shaping

conservation actions for an entire population. Further, the new analytical methods applied to ecologically complex data will be important to any study that uses long-term marking. Avian populations are predicted to become more threatened in the future, so it is increasingly critical to understand factors driving vital rates and to develop approaches to alleviate threats to population persistence.

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Preface

Effective conservation of small populations requires in-depth knowledge of factors affecting reproduction, survival, and recruitment into the breeding population (i.e., vital rates). This degree of detail is best achieved through long-term annual marking and monitoring of individuals throughout their entire breeding range. Great Lakes piping plovers have been marked with unique leg band combinations since 1993 and rigorously resighted along more than 5,000 km of shoreline. The knowledge of individuals' genealogies and breeding histories provided by these data has allowed me to answer novel life-history questions in my dissertation. Few such comprehensive datasets on abundances and vital rates exist for other rare or endangered species (Beissinger et al. 2006).

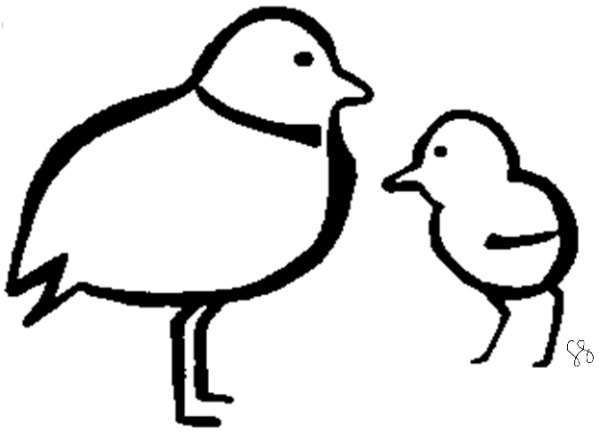
At the heart of my research is the fundamental question: How can studying variation within and among individuals be used to conserve a population effectively? I aim to improve management of the piping plover by answering this question using both long-term banding data (Chapters 1-3) and experimental study (Chapter 4). This dissertation is composed of four separate investigations into the drivers of: (1) reproductive success, (2) phenotypic variance of fitness-related traits, (3) age-specific survival and recruitment, and (4) the lower survival rates of captive-reared piping plover chicks compared to wild-reared chicks. Together, these four chapters provide a more comprehensive framework for analyzing data on marked individuals with the all-encompassing goal of shaping conservation actions for an entire population.

This dissertation is not written in the first person, as it is a compilation of four manuscripts already published. As such, the formats of the four chapters differ slightly

according to the requirements of the journals for which they were intended. Chapter 1, 'Female site familiarity increases fledging success in piping plovers', was published in *The Auk* in 2012. Chapter 2, 'Genetic and environmental influences on fitness-related traits in an endangered shorebird population' was published in *Biological Conservation* in 2014. Chapter 3, 'Age-specific survival and recruitment of piping plovers in the Great Lakes region was published in *Journal of Avian Biology* in 2014. Chapter 4, 'Auditory and visual threat recognition in captive-reared Great Lakes piping plovers' was published in *Applied Animal Behaviour Science* in 2013.

CHAPTER 1

FEMALE SITE FAMILIARITY INCREASES FLEDGING SUCCESS IN PIPING PLOVERS (*CHARADRIUS MELODUS*)



ORGANISMS THAT REPRODUCE repeatedly throughout their lifetimes often have age-specific patterns of reproductive success (Forslund and Pärt 1995). In birds, reproductive performance typically improves with age in younger age classes, often followed by a senescent decline in older individuals (Nur 1984, Forslund and Pärt 1995, Fowler 1995, Newton and Rothery 2002). Four general hypotheses have been raised to explain increased reproductive performance with age among younger age classes. The selection and recruitment hypotheses address population-level changes that occur as a result of selective mortality or recruitment of individuals at the population level, whereas the breeding experience and restraint hypotheses propose improvements in reproductive performance that can occur within individuals.

The selection hypothesis (Curio 1983) proposes that the positive relationship between age and reproductive success occurs through the selective loss of poor breeders (Forslund and Pärt 1995, Mauck et al. 2004, Steenhof and Heath 2009), whereas the recruitment hypothesis predicts that increased reproductive performance is due to later recruitment of high-quality breeders (Forslund and Pärt 1995, Martin 1995, Steenhof and Heath 2009). Both of these hypotheses are attributable to variation among individuals and depend on positive correlations in life-history traits among individuals: fecundity with survival in the case of the selection hypothesis and fecundity with age at first breeding for the recruitment hypothesis (Mauck et al. 2004).

In addition to age-related improvements within cohorts, two categories of hypotheses address age-related improvements that occur within individuals: (1) age-related improvements in competence (i.e., amelioration of constraints or improvement of breeding experience) and (2) age-related changes in allocation of reproductive effort (i.e.,

restraints; Curio 1983, Forslund and Pärt 1995, Martin 1995, Steenhof and Heath 2009). The breeding experience hypothesis posits that the effects of previous breeding experience may improve later breeding performance, either because of more efficient physiological processes or fine tuning of behaviors closely associated with reproduction (Pärt 1995). Thus, previous experience in activities such as laying and incubating eggs, brooding offspring, or tending young may lead to increased reproductive performance by older birds if such behaviors can be learned and therefore improve with accumulated experience (Pyle et al. 1991). Shared breeding experience of pairs is an important component of this hypothesis because it enables individuals to gain knowledge about how to effectively coordinate incubation and brood-rearing duties with previous mates (Haig and Oring 1988, Mauck et al. 2004). Potential improvements are not limited to breeding experience, however; older birds may be more productive because of improvements in behaviors not directly associated with reproduction, such as feeding skills, intraspecific competition, or predator avoidance (Nol and Smith 1987, Wooller et al. 1990, Weimerskirch 1992, Brown and Roth 2009). Such age-related improvements seem most likely to explain the evolution of deferred breeding, particularly in birds with complex foraging behaviors (Burger 1980, Marchetti and Price 1989). For young birds, reproductive effort likely accentuates patterns caused by constraints; as birds gain experience and become more likely to succeed in reproduction, their allocation of effort to reproduction should also increase (Forslund and Pärt 1995, Mauck et al. 2004). As an individual's experience increases, the return per unit effort increases; thus, effort should increase with age and experience (Mauck et al. 2004). But as individuals approach senescence and survival or reproductive abilities decline, the restraint hypothesis also

predicts that older individuals should invest more heavily in current reproduction because they have declining reproductive value (Forslund and Pärt 1995, Brown and Roth 2009, Steenhof and Heath 2009).

In addition to these direct potential influences on fledging success, age and experience can indirectly enhance reproductive performance through their influence on arrival and breeding times (Roche et al. 2008, Brudney 2009). Older, more experienced birds typically nest earlier in the breeding season (Oring and Lank 1982, Hatch and Westneat 2007, Garcia-Navas and Sanz 2011) and are likely to have the greatest amount of prior breeding experience and site familiarity. Because reproductive performance typically declines seasonally in birds (Rohwer 1992, Brinkhof et al. 2002), earlier breeding can lead to further increases in reproductive success for older and more experienced birds.

Despite numerous investigations, the degree to which age, individual experience, and their interactions affect variation in timing of breeding and fledging success remains unclear (Nol and Smith 1987, Pyle et al. 1991, Martin 1995, Pärt 1995, Mauck et al. 2004). The rarity of large samples of marked individuals of both known age and known experience, further confounded by strong correlations between age and breeding experience, have made it difficult to determine whether improvements in reproductive performance are caused by breeding experience or other age-related factors (Brown and Roth 2009). Our study uses 17 years of data (1993–2009) on piping plovers (*Charadrius melodus*) breeding in the Great Lakes region of North America to explore causes of age-related variation in timing of breeding and fledging success. The Great Lakes piping plover population is almost completely marked and monitored, with >90% of nesting

adults and >95% of offspring individually banded (Roche et al. 2008), and annual detection probabilities of breeding birds approaching 100% (LeDee et al. 2010), which allows the development of detailed reproductive histories for most individuals in the population. Although age, breeding experience, nest location experience, and pair-bond experience tend to be positively correlated, their effects are not indivisible because piping plovers begin breeding at different ages and have varying degrees of mate and site fidelity (Haig and Oring 1988, Roche et al. 2008, Gratto-Trevor et al. 2010). Here, we exploit this variability in individual histories to determine which of the following four factors have the greatest influence on timing of breeding and fledging success: (1) physiological or behavioral maturation, which represents improvements due to age per se, regardless of prior breeding experience; (2) prior breeding experience, which may allow for the development of individual breeding skills, such as incubation and rearing of offspring; (3) prior site experience, which may provide local knowledge, such as safe nesting sites or improved foraging sites; and (4) prior mate experience, which may aid in the coordination of incubation and brood-rearing duties among pair members. By using random effects models to assess among-individual variation in these parameters, we also address the potential for selective mortality or deferred recruitment to produce these patterns.

METHODS

Focal species and study area.—The piping plover is a small shorebird endemic to North America and restricted to three breeding populations: Atlantic Coast, Great Plains, and Great Lakes (Haig et al. 2005). The Great Lakes population of piping plovers nests on wide, sparsely vegetated sand and cobble beaches along the shoreline of lakes Michigan,

Superior, and Huron (U.S. Fish and Wildlife Service [USFWS] 2003); most of the population occurs in Michigan. Listed as federally endangered in 1986 (USFWS 1985), the Great Lakes population has numbered from 17 to 71 known breeding pairs (F. J. Cuthbert and S. P. Saunders, unpubl. data). Females typically produce a four-egg clutch, offspring are precocial, and both parents assist in rearing young. Females, however, are more prone to abandon the brood prior to fledging (Cairns 1982). Nests are covered with wire exclosures to reduce egg predation as soon as they are discovered (Melvin et al. 1992), and recreational activities are managed to reduce human disturbance in nesting and brood-rearing areas (USFWS 2003). Our study used data from known nesting locations between 1993 and 2009 (Fig. 1).

Field data collection.—Since 1993, surveys for breeding pairs of piping plovers have been conducted at the beginning of each breeding season at historical, recent, and potential nesting habitats. Most breeding pairs were monitored every 1 to 4 days from nest initiation until the nest was destroyed or abandoned or until young disappeared or fledged. Data collected during monitoring included identity of piping plover pairs (based on unique color bands; Wemmer et al. 2001) and number of eggs or offspring present at each visit. Approximately 98% of individuals were of known age, and the remaining 2% were assigned minimum ages of 1 the first time they were recorded breeding.

Data summary and analyses.—We defined fledging success as the number of offspring per brood that survived to fledging age (~23 days old; Brudney 2009), based on pairs that hatched at least one young. We used fledging success for pairs that hatched at least one egg because nearly all nests were protected by predator exclosures during our study period (100% of nests were exclosed from 2004– 2009), as mandated under our

Federal Endangered Species Permit. Thus, hatching success was not a reliable measure of reproductive performance because it primarily reflected how quickly and effectively nests were found and fenced by investigators, rather than varying levels of parental investment. Nests where fledgling count was not recorded were excluded from analyses, as were nesting attempts where the identity and experience of at least one pair member was unknown (n = 415, representing 71% of all nests monitored during our study period). We defined a pair as a male and female piping plover that mated, produced eggs, and shared incubation of a nest (n = 320 unique pairs comprised of 181 females and 183 males).

Previous studies have demonstrated substantial spatial variation in survival of plover young (Colwell et al. 2007, Le Fer et al. 2008, Brudney 2009), and we wished to control for this source of variation in our analyses. We defined a breeding location as a single, continuous stretch of appropriate nesting and brood-rearing habitat (mean ± SD = 3.33 ± 2.89 km; n = 20) separated from other sites by >1.5 km of inhospitable shoreline (Fig. 1; Wemmer et al. 2001, Haffner et al. 2009). Our measures of location experience utilized these same definitions and refer to an individual's or pair's familiarity with one of these 20 breeding locations, but not necessarily to a specific nesting territory or home range (Haffner et al. 2009). Because locations differed from each other in terms of offspring survival (Brudney 2009), we added location to our statistical models as an *a priori* random effect (Zuur et al. 2009). Similarly, we added male and female identity as second and third random effects to account for pseudoreplication of individuals (Zuur et al. 2009) and to test for among-individual variation in reproductive performance as posited by the selection and recruitment hypotheses (van de Pol and Verhulst 2006).

We initially used two different methods to tally breeding and location experience. The first method was based on all nesting attempts, including renests, and allowed breeding experience to accumulate within a single breeding season. By this measure, individual experience was the sum of all known nesting attempts that an individual had made in its lifetime, location experience was the sum of all nesting attempts at a particular breeding location, and pair experience was the sum of all nesting attempts that these two piping plovers had made together. Hence, a pair of yearling piping plovers that nested together for the first time and had two failed nesting attempts at location A prior to hatching their third nest at location B would receive values of 1 each for age, 3 for individual and pair breeding experience, and 1 for location experience when evaluating their third nesting attempt. The second method tallied only annual breeding experience, where (1) breeding experience increased only if a given individual or pair nested in a previous year and (2) location experience increased only if a given individual or pair nested at the same location in a previous year (in the above example, all measures would be coded as 1). We found that the annually based covariates were better predictors of fledging success than their within-season complements in all cases, and we therefore based all measures of breeding and location experience on the second method, which tallied only annual breeding experience. We also tallied instances when individuals either changed breeding locations or changed mates between years to directly assess the effects of moving to a new breeding location or breeding with a new partner.

We used generalized linear mixed models (package lme4) in R, version 2.12.0 (Bates and Sarkar 2006), to investigate sources of variation in hatch date (HDATE, where 1 = 1 June; modeled using a normal distribution) and fledging success (FLEDGE, range:

0–4 fledged young per brood; modeled using a Poisson distribution). For each response variable (HDATE or FLEDGE), we considered 12 potential covariates: (1) female age (AGEF), (2) female breeding experience (EXPF), (3) female location experience (LEXPF), (4) female mate change (FMACH = 1 if new mate, 0 if previous mate), (5) female location change (FLOCH = 1 if new location, 0 if previous location), (6) male age (AGEM), (7) male breeding experience (EXPM), (8) male location experience (LEXPM), (9) male mate change (MMACH), (10) male location change (MLOCH), (11) pair breeding experience (EXPP), and (12) pair location experience (LEXPP; Table 1).

Because individual covariates were highly correlated with each other, we used a forward selection approach to model-fitting to minimize problems with autocorrelation. For both the hatch date and fledge analyses, we began with a null model that included an intercept, random location effect, and random individual effects for both males and females. To this model we added each of the 12 covariates individually and ranked these models on the basis of Akaike's information criterion corrected for small sample size (AIC_c). After each step, we discarded any uninformative covariates that led to increased AIC_c scores (Arnold 2010). If multiple covariates yielded a reduction in AIC_c compared to the null model, the model with lowest AIC_c was used as a base model for considering additional undiscarded covariates. If the linear term for a given covariate was selected, we also considered the quadratic term (e.g., age^2); if two or more covariates were selected, we also evaluated interaction terms. When additional covariates no longer led to a reduction in AIC_c, the best-supported model from the previous step was retained as the top supported model. Means are reported ± SD unless otherwise indicated.

RESULTS

The mean hatch date was 20 June ± 13 days (90% range: 25 May–16 July), and the mean number of young fledged per brood was 2.0 ± 1.42 offspring (variance = 2.02). Although the variance was identical to the mean, fledging success was not distributed as a perfect Poisson variable (χ^2 = 114.0, df = 4, $P < 0.0001$) because of excessive numbers of piping plover nests that fledged zero or four offspring. On average, males initiated nesting at an older age than females (males: 1.54 ± 0.75 years, n = 149; females: 1.32 ± 0.60 years, n = 146; t = 2.90, df = 293, P = 0.004), and males also bred for more years than females (Table 2). Sample sizes were adequate (n = 10 to 180) for individual-based measures of age and experience out to 5–7 years and for pairs out to 3 years. Location- specific sample sizes ranged from a low of 1 nest at High Island to 73 nests at Sleeping Bear Dunes.

Fledging success declined with hatch date (regression equation: FLEDGE = 0.92 [SE = 0.07] – 0.012 [SE = 0.003] × HDATE; n = 415). The best-supported model for hatch date included linear and quadratic terms for both female and male ages. As piping plovers aged, both females and males nested earlier in the season; however, the effect was stronger among females and diminished among older age classes (Fig. 2). After accounting for female and male ages, no other covariates were related to hatch date. The best-supported model for fledging success included female location experience, female location change, and their interaction (FLEDGE = 0.56 [SE = 0.08] + 0.07 [SE = 0.03] × LEXPF + 0.11 [SE = 0.22] × FLOCH – 0.24 [SE = 0.14] × LEXPF × FLOCH; Table 3). Fledging success increased with accumulated location experience of the breeding female and suffered a substantial setback when females moved to a new location (Fig. 3).

Random location effects indicated that fledging success was greater, on average, at Sleeping Bear Dunes and lower at Cross Village (Fig. 4A), whereas hatching dates were earlier at Sleeping Bear Dunes and later at Vermilion (Fig. 4B). Individual random effects were strongly supported for hatch date ($\sigma_{FEMALE} = 12.35 \pm 3.51$; $\sigma_{MALE} = 5.91 \pm 2.40$), but not for fledging success (both estimates were zero).

DISCUSSION

Previous studies have documented seasonal declines in reproductive success for piping plovers in the Great Plains and Atlantic populations (Knetter et al. 2002, Harris et al. 2005, Cohen et al. 2009), similar to what we found for Great Lakes piping plovers. Such declines are widespread in birds (Daan et al. 1988, Rohwer 1992, Brinkhof et al. 2002) and are often driven by seasonal declines in clutch size (Daan et al. 1988, Hochachka 1990). Although piping plovers lay fewer eggs in late-season nesting attempts (Cohen et al. 2009), most clutches contain four eggs, regardless of initiation date. For piping plovers, greater rates of nest predation and partial or total brood losses are more likely responsible for declining reproductive success in late-nesting pairs (Roche et al. 2008, Brudney 2009, Cohen et al. 2009). Seasonally declining offspring survival may be a result of deteriorating environmental conditions, such as decreases in food abundance (Van der Jeugd et al. 2009), or seasonal changes in abundance or behavior of predators could lead to greater predation risks for late-hatched broods (Kruse et al. 2001). Alternatively, seasonally declining survival might be correlated with differences in parental quality, with older, more experienced adults breeding earlier in the season (Garcia-Navas and Sanz 2011), a pattern that was strongly supported by our data.

We found that timing of breeding was strongly influenced by male and female ages, but not by prior breeding or location experience. These results corroborate conclusions from numerous other studies (Nur 1984, Nol and Smith 1987, Forslund and Pärt 1995), all of which suggest that older birds nest earlier in the breeding season than younger ones. Female age had a stronger effect on hatch date than did male age, with females nesting earlier in the season than males among the oldest age classes. During nearly every breeding season in recent years, numerous (about 8–15) unpaired males and few (about 1–3) unpaired females were observed (F. J. Cuthbert and S. P. Saunders, unpubl. data). Thus, older females are not limited by availability of mates and are able to initiate nesting immediately after arrival on the breeding grounds. By contrast, older males must frequently wait for a potential mate and end up breeding with younger and later-nesting females. Although neither male nor female age was an important predictor of fledging success, both were important predictors of hatching date, and because earlier-hatched broods were more successful, timing of hatching nevertheless translates into enhanced fledging success for early-season breeders. Several possible mechanisms can explain why age might affect timing of breeding so strongly but have no bearing on fledging success. First, timing of breeding is often dictated by arrival times, and older, more experienced birds frequently arrive earlier than younger birds (Oring and Lank 1982, Nol and Smith 1987, Forslund and Pärt 1995, Potti 1998, Colwell et al. 2010). This may be because younger, more inexperienced birds arrive when the competition from established birds is reduced (Oring and Lank 1982). Also, older birds may have more foraging experience and, therefore, be in better condition on the wintering grounds,

allowing them to migrate and nest earlier (Alisauskas and Ankney 1985, Forslund and Pärt 1995, Morrison et al. 2007).

Female location familiarity was the most important predictor of fledging success, even though site fidelity in piping plovers is male-biased (Haig and Oring 1988). In socially monogamous shorebirds, fidelity to a specific nesting location is generally male-biased because males locate and defend territories before females arrive (Johnson et al. 1993, Flynn et al. 1999). In semipalmated plovers (*C. semipalmatus*), returning adult males nearly always settled on the same or an adjacent territory in successive breeding seasons, whereas females were able to choose among multiple breeding opportunities and were less likely to return to the nesting territory used in previous years (Flynn et al. 1999). Similarly, female piping plovers are more likely to change nesting locations after reproductive failure, whereas males often return to breed on the same territory every year, regardless of previous reproductive failure (Haig and Oring 1988). As in other plovers (Warriner et al. 1986), female piping plovers often abandon their broods and depart on fall migration earlier than males (Cairns 1982). As a result, female site fidelity is weaker at both the beginning and the end of the breeding season (Flynn et al. 1999). Because females use more locations than males, there is greater potential for females to learn which locations are best for raising young and to return to these locations in subsequent years (Haig and Oring 1988, Rioux et al. 2011). Hence, females are more likely to acquire location experience at sites where they have had previous success in reproduction. This interpretation was further supported in the present study by the importance of female location change as the second and only other predictor of fledging

success. On average, females that moved to a new location experienced a decrease in fledging success from 2.1 to 1.5 chicks.

Familiarity with a nest-site location is considered valuable because it facilitates food exploitation, territory defense, and predator avoidance (Wiens and Cuthbert 1988), but it is not clear why these same benefits would not also accrue to males. Although males also gain site familiarity from reuse of previous sites, their fidelity to potentially poor territories may preclude development of a strong correlation between site familiarity and fledging success (Cohen et al. 2006). In addition, there was no apparent benefit from year-to-year mate retention in our study. Haig and Oring (1988) found that 71% of surviving piping plovers returned to their former breeding sites, whereas only 19% repaired with the same mate, although former mates were present. Similarly, Wiens and Cuthbert (1988) demonstrated that 84% of all returning piping plovers at Lake of the Woods nested within 200 m of their previous nest site, but only 45% of pairs reunited when both male and female were present the next season.

CONCLUSIONS

Our analysis suggests that most improvements in reproduction with age in piping plovers occur within individuals, and not at the population level. For fledging success, individual random effects were not significant, indicating no consistent variation among individuals in reproductive performance. Such among individual variation is essential to the selection and recruitment hypotheses (Mauck et al. 2004). Although hatch date varied among individuals, our analysis showed that hatch date also improved with age within individuals. Finally, our results provide strong evidence that individual experience with a breeding location is the primary driver for increased reproductive success with age in

piping plovers. This result supports the breeding experience hypothesis, indicating that previous experience, with nesting sites in this case, can improve later reproductive performance. Female familiarity with nest-site locations significantly influenced fledging success, implying that knowledge and behaviors not directly associated with reproduction enhance piping plover fledging success. We believe that female experience at a given nest site could account for variation in reproductive success in other widely distributed species of birds as well. Additionally, male and female ages are significant predictors of hatch date, which, in turn, is a significant predictor of fledging success.

These findings have important conservation implications for management of this endangered population. For example, early-laid nests are likely to fledge more young, and these young are also more likely to survive their first winter (Roche et al. 2008), emphasizing the importance of finding and protecting the earliest nests so that they hatch successfully. Our results also emphasize the importance of protecting established breeding sites where piping plovers can accrue breeding experience over multiple years. Any human disturbance event such as beach grooming, public recreation, and pets off leash (F. J. Cuthbert and S. P. Saunders, unpubl. data), as well as anthropogenic flooding of beaches (Gratto-Trevor and Abbott 2011), can prevent piping plovers from acquiring location experience that will allow them to maximize their fledging success.

TABLE 1. Variables used to estimate hatch date and fledging success of Great Lakes piping plover pairs during 1993–2009. Variables are organized according to the type of experience that each describes: age, prior site experience, prior breeding experience, and prior mate experience. The quadratic form of these variables (e.g., $AGEF^2$) was also included in the models. Fledging success (FLEDGE) and hatch date (HDATE) were the response variables. Nest-site location (LOCATION) and individual identity (IDF and IDM) were included as random effects in all models.

Experience	**Variable**	**Definition**
	FLEDGE	Fledging success; the number of chicks per brood that survived to fledging age
	HDATE	Hatch date of first egg in clutch (1 = 1 June)
	LOCATION	Nest site location
	IDF	Unique female identification number
	IDM	Unique male identification number
Age-related	AGEF, $AGEF^2$	Age of female within a pair
	AGEM, $AGEM^2$	Age of male within a pair
Site-related	LEXPM, $LEXPM^2$	Male's location experience, measured annually
	LEXPF, $LEXPF^2$	Female's location experience, measured annually
	FLOCH	Nesting location change by female
	MLOCH	Nesting location change by male
Breeding-related	EXPM,$EXPM^2$	Number of years male has nested
	EXPF, $EXPF^2$	Number of years female has nested
Mate-related	EXPP,$EXPP^2$	Number of years a given pair has nested together
	LEXPP, $LEXPP^2$	Pair's location experience, measured annually
	FMACH	Mate change by female
	MMACH	Mate change by male

TABLE 2. Number of brood-rearing attempts by Great Lakes piping plover pairs from 1993–2009, according to male and female age. Individuals appear multiple times if they nested successfully in >1 year.

	Female age										
Male age	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	∑
1	47	20	6	9	1	1	-	1	1	-	**86**
2	30	31	15	7	4	2	3	-	-	-	**92**
3	13	27	19	8	6	3	2	2	-	-	**80**
4	9	14	13	11	8	-	-	-	-	-	**55**
5	4	4	8	6	7	4	-	1	-	-	**34**
6	-	5	5	6	5	3	2	-	-	-	**26**
7	1	1	3	2	5	3	2	1	1	-	**19**
8	1	-	1	3	-	2	1	1	-	1	**10**
9	1	1	-	-	-	-	-	1	1	-	**4**
10	-	-	1	-	-	1	1	-	1	-	**4**
11	-	1	-	2	-	1	-	-	-	-	**4**
12	-	-	1	-	-	-	-	-	-	-	**1**
∑	**106**	**104**	**72**	**54**	**36**	**20**	**11**	**7**	**4**	**1**	

TABLE 3. Model rankings for top-supported models used to estimate fledging success (FLEDGE) for Great Lakes piping plover pairs from 1993–2009. Models were ranked according to differences in Akaike's information criterion (ΔAIC_c) and Akaike weights (w_i). Important covariates for females (F), males (M), and pairs (P) included location experience (location), location change (lchange), and an interaction term (F location × F lchange). All models included an intercept term as well as location, male identity, and female identity as random effects on the intercept (k = 4 parameters).

Model	**ΔAIC_c[a]**	**Deviance**	***N* parm**	**Model weight**
F location + F lchange + F location×F lchange	0.00	508.2	7	0.50
F location + F lchange	1.10	511.3	6	0.29
F location	3.90	516.1	5	0.07
F lchange	4.20	516.4	5	0.06
F location + M lchange	4.80	515.0	6	0.05
P location	6.40	518.6	5	0.02
Null model	8.60	522.8	4	0.007

[a]AIC_c of the top model was 522.2.

FIGURE 1. Distribution of Great Lakes piping plover nest-site locations during 1993–2009. Asterisk indicates that the Cross Village (CV) location also includes Bliss and Sturgeon Bay, which are within 1.6 km of each other.

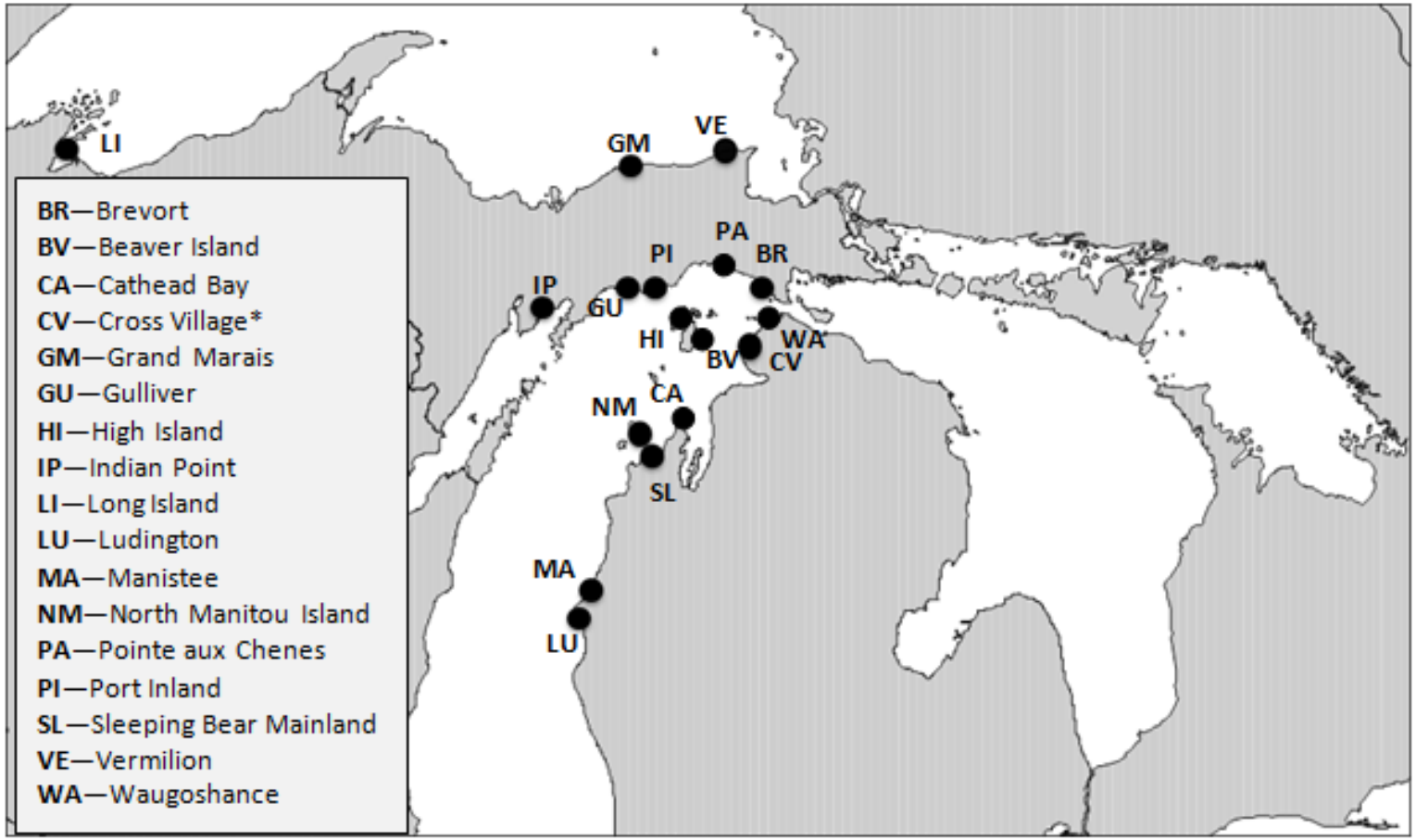


FIGURE 2. Effects of female (n_f = 181) and male (n_m = 183) ages on hatch date (1 = 1 June) during 1993–2009 in the Great Lakes region, excluding renesting attempts. Solid regression line represents the linear model where hatch date was modeled as a function of male and female age, with male age held constant. The dashed regression line represents the model where female age was held constant. HDATE = $\beta_0 + \beta_1 \times \text{agef} + \beta_2 \times \text{agef}^2 + \beta_3 \times \text{agem} + \beta_4 \times \text{agem}^2$, where $\beta_0 = 36.5 \pm 1.83$ [SE], $\beta_1 = -5.12 \pm 0.83$, $\beta_2 = 0.37 \pm 0.09$, $\beta_3 = -2.75 \pm 0.71$, and $\beta_4 = 0.21 \pm 0.07$. Dotted lines indicate ± SE.

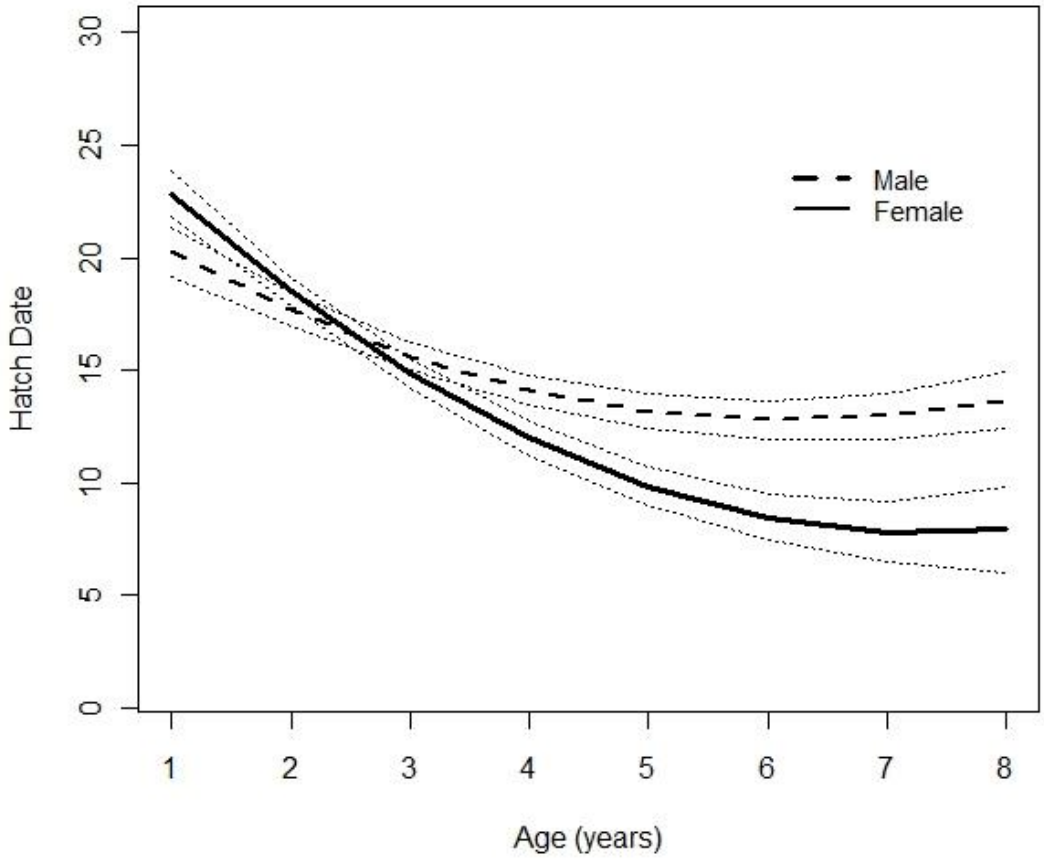


FIGURE 3. Effects of female location experience and female location change on fledging success of piping plovers in the Great Lakes population. Solid regression line represents fledging success as a function of female location experience and the interaction term, for females that did not change locations (i.e., female location change held constant at FLOCH = 0). The dashed regression line represents fledging success for females that did change locations (i.e., female location change held constant at FLOCH = 1). Dotted lines indicate ± SE. Graphs include 95% of the observed range of variation in female location experience. FLEDGE = 0.56 ± [SE = 0.08] + 0.07 [SE = 0.03] × LEXPF + 0.11 [SE = 0.22] × FLOCH – 0.24 [SE = 0.14] × LEXPF × FLOCH.

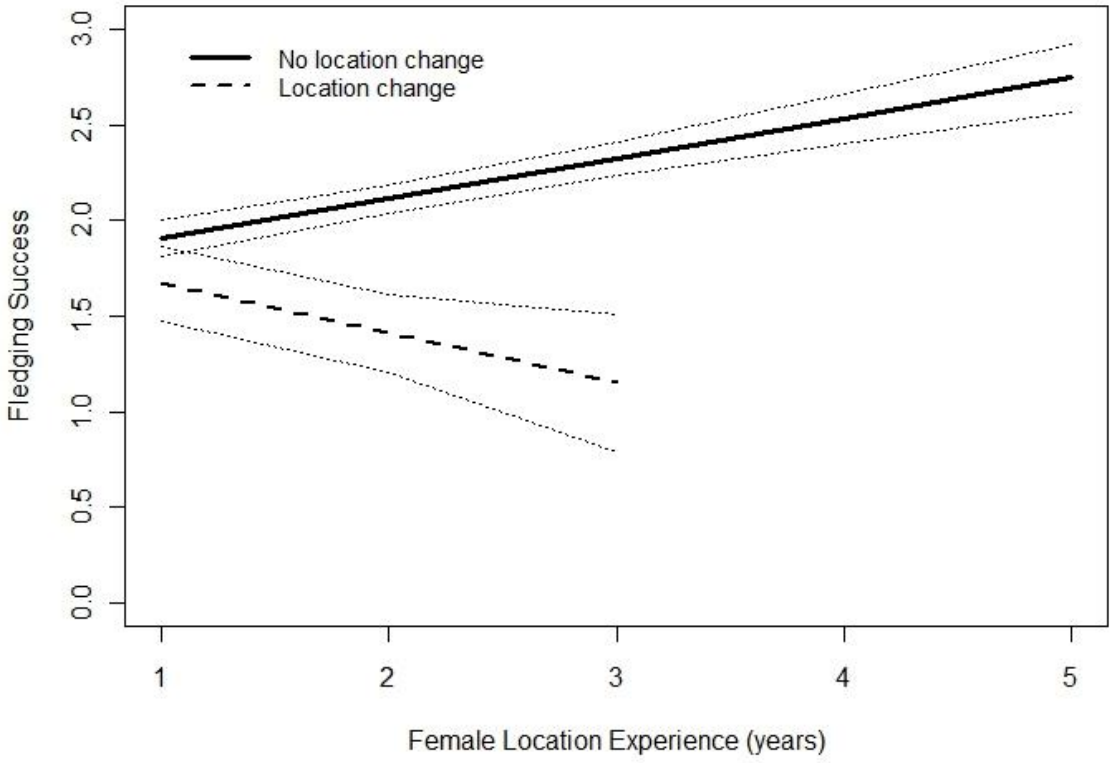
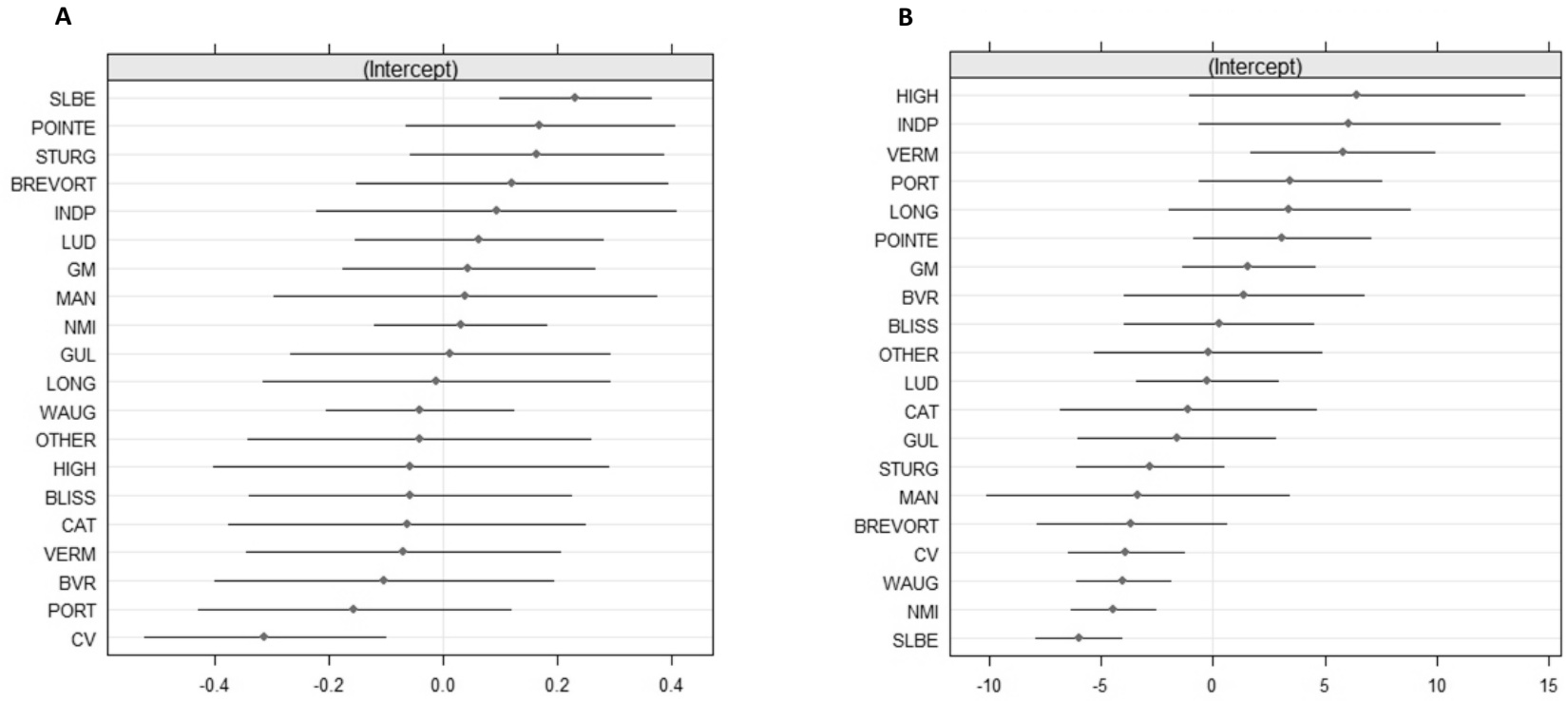
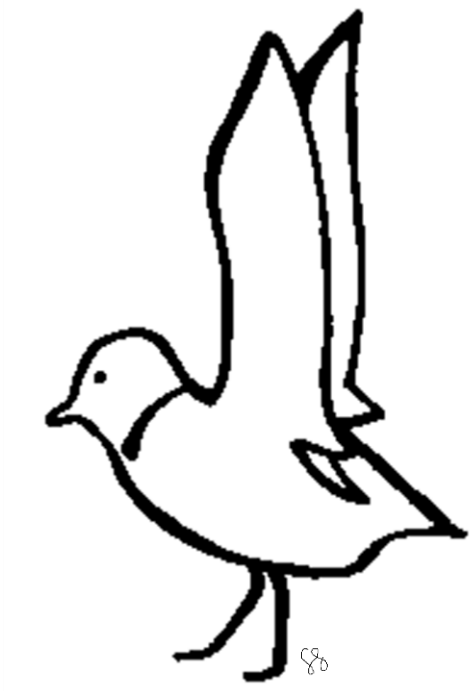


FIGURE 4. Prediction intervals of the random location effect on (A) fledging success and (B) hatch date. Breeding sites are listed on the *y*-axis of both figures, and their influence (either positive or negative) on each response variable is shown along the *x*-axis. In panel A, all locations overlap zero except for SLBE (Sleeping Bear Dunes, greater success) and CV (Cross Village, lower success). In panel B, all except 5 sites overlap zero; birds at 4 sites, including Sleeping Bear Dunes, nested earlier than average, whereas birds at Vermilion (an upper peninsula site) nested later than average. See Figure 1 for nest-site locations and abbreviations (STURG = Sturgeon Bay).



CHAPTER 2

GENETIC AND ENVIRONMENTAL INFLUENCES ON FITNESS-RELATED TRAITS IN AN ENDANGERED SHOREBIRD POPULATION



NEARLY EVERY ALTERATION to a population's environment, whether it is natural or anthropogenic, is a potential source of new or intensified directional selection on traits important for fitness (Gienapp et al., 2008). Responses of populations to such challenges include dispersing to a new location, adjusting the phenotype non-genetically (i.e., phenotypic plasticity), adapting via genetic changes through evolution, or extirpation (Serbezov et al., 2010). While dispersal may lead to local extirpation, but persistence elsewhere, plasticity and adaptation can prevent local extinction. Phenotypic plasticity may enhance short-term persistence of populations as the environment changes, but there are limits to plastic responses and they are unlikely to provide long-term persistence in the face of continuous directional environmental change (Gienapp et al., 2008), such as habitat loss and global climate change. Persistence through major, lasting environmental changes depends on adaptation, with its rate dependent on the additive genetic variance for fitness-related traits. Although genetic variability may be less critical than other determinants of population persistence in the short-term, it can play a decisive role in ultimately allowing a population to persist in and adapt to a changing environment; thus, extirpation is the final consequence of the inability of a population to adapt with sufficient speed to novel conditions (Falconer et al., 1996; Lande and Shannon, 1996).

Because an evolutionary response is necessary for long-term viability of wild populations, disentangling the genetic and environmental influences on morphological and life-history traits is becoming increasingly pertinent to conservation (Lane et al., 2011). Due to the relative ease with which parents and their offspring can be marked and identified, studies of bird populations have played an important role in the application of quantitative genetic methods to natural populations (Merilä and Sheldon, 2001).

However, although more than 30 years of research into the genetics of wild bird populations suggests that life-history traits are to some extent heritable, little is still known about how quantitative genetic parameters vary among traits, populations, and species (Postma and Charmantier, 2007). This study uses long-term data from a natural shorebird population to quantify the genetic and environmental components of variance of three fitness-related traits: age-corrected chick body mass, natal dispersal distance, and female timing of breeding.

Body mass is an important component of parental and offspring fitness in many vertebrate species (Haramis et al., 1986; Festa-Bianchet et al., 1998; Saunders et al., 2014). Although there is considerable evidence that skeletal measures of body size are heritable in wild animal populations, it is often assumed that the non-skeletal component of body weight is determined primarily by environmental factors, such as nutritional status (Merilä et al., 2001). Yet analyses of cross-fostering experiments of collared flycatchers (*Ficedula albicollis*) and blue tits (*Parus caeruleus*) suggest a significant genetic component to variation in relative body weight as well (Merilä et al., 1999, 2001).

Natal dispersal, defined as the movement of an individual from its natal site to a new site for first breeding, is a major component of gene flow and therefore another important trait for adaptation of populations. Evolution of natal dispersal has frequently been attributed to the social and environmental context faced by individuals (e.g., inbreeding avoidance, resource competition; Charmantier et al., 2011), but heritability estimates for vertebrates are still limited (but see: Massot and Clobert, 2000; Hansson et al., 2003; Gienapp and Merilä, 2010). This scarcity is largely due to the need to obtain estimates from realized dispersal events over sufficiently large spatial and temporal

scales (Doligez et al., 2012), which can be challenging because of the need to track an unbiased sample of parent and offspring movements.

Timing of breeding is an important fitness-correlated trait as it is the main determinant of the time a migratory bird has available for raising young (Pulido et al., 2001). It further determines the fitness of offspring, as earlier breeding leads to more time for chick growth prior to autumn migration (Harris et al., 1994). Seasonal declines in chick survival, and consequently reproductive success, have been documented in numerous precocial species (Guyn and Clark, 1999; Traylor and Alisauskas, 2006; Brudney et al., 2013; Catlin et al., 2013).

Quantitative genetic models (Falconer et al., 1996) allow estimation of components of variance observed in a phenotypic trait by jointly analyzing data on the trait and genealogical relationships in a pedigree. Specifically, the 'animal model' approach allows simultaneous estimation of components of variance that can be attributed to genetic, environmental, and other unknown factors (Shaw, 1987; Kruuk, 2004). Heritability of the phenotypic trait can then be estimated from the fraction of the variance that can be attributed to the additive genetic effects. Only recently has the animal model framework been used for wild animal and plant populations, resulting in applications to conservation issues (e.g., harvesting strategies, habitat fragmentation effects) and management for species of conservation concern (Coltman et al., 2003; Stockwell et al., 2003; Law and Stokes, 2005).

Teasing apart the genetic and environmental underpinnings of fitness-related traits in piping plovers (*Charadrius melodus*) will help identify which have the greatest potential to evolve relative to other traits, allowing for more accurate predictions of the

impact of local and global environmental changes on the long-term persistence of this endangered population. Because of their endangered status, piping plovers in the Great Lakes region of North America are thoroughly monitored throughout the entire known breeding range, so young are likely to be encountered even if they disperse to a new breeding location (LeDee et al., 2010). Additionally, the resighting probability of breeding adults is near perfect (LeDee et al., 2010); thus, individuals that return to breed will likely be encountered. This intensive monitoring makes the Great Lakes piping plover population ideal for accurately estimating heritabilities of natal dispersal distance and timing of breeding in particular.

We used long-term (1994–2013) phenotypic records from mark-recapture data and a multi-generational social pedigree to examine the quantitative genetic influences on three fitness-related traits in the Great Lakes piping plover population. Our objectives were to: (1) estimate the heritabilities of chick mass, natal dispersal distance, and female timing of breeding; (2) quantify the genetic and environmental variance components of these traits; and (3) determine the evolvability of each trait as measured by the coefficient of additive genetic variation. Results from this study will help predict the short- and long-term consequences of climate change to an endangered population, as well as identify management priorities, given the relative contributions of genetic and environmental influences on traits essential to fitness.

METHODS

Focal species and study area.—The Great Lakes population of piping plovers nests on wide, sparsely vegetated sand and cobble beaches along the shoreline of lakes Michigan, Superior, and Huron (U.S. Fish and Wildlife Service [USFWS], 2003), and winters

primarily along the U.S. Atlantic coastline from North Carolina to Florida and the Bahamas (Stucker et al., 2010; Gratto-Trevor et al., 2012). Since being listed as federally endangered in 1986 (USFWS, 1985), the population has fluctuated between 17 and 71 known breeding pairs (Saunders et al., 2014). Females typically produce a four-egg clutch, and both parents incubate and assist in rearing precocial young. Nests are protected by wire exclosures to reduce egg predation (Melvin et al., 1992) and recreational activities are managed to reduce human disturbance in breeding areas (USFWS, 2003). This study used data from all known nesting locations during 1994–2013 (Fig. 1).

Field data collection.—Surveys were conducted at historical, recent, and potential nesting sites to locate breeding pairs. Plovers were banded using U.S. Geological Survey (USGS) aluminum bands and Darvic color bands (Avinet Inc., Dryden, NY, USA). Unmarked or brood-marked (i.e., previously marked as chicks) incubating adults were trapped on the nest (Lincoln, 1947), sexed, and given unique color band combinations. Chicks were caught by hand, weighed with a Pesola spring scale to the nearest gram, and given brood-specific color band combinations, typically at 5–15 days of age (Roche et al., 2010a). Because all nesting sites were monitored throughout the breeding season, hatch dates were known and therefore, the age of every chick was known. Breeding pairs were monitored every one to four days from nest initiation until all chicks disappeared or fledged. Data collected during monitoring included identity of plover pairs (based on individual color bands), locations of nests, hatch dates, and numbers of chicks that survived to fledging age.

Data summary and pedigree construction.—Similar to body condition, we assumed that relative age-specific chick body mass was a good indicator of survivability (Saunders et al., 2014). We calculated the residual body mass (hereafter referred to as chick mass) as the residuals from a regression of $\log_e$-body mass on known age at banding (to account for differences in body size associated with age; Schulte-Hostedde et al., 2005). Because structural measurements of chicks were not available, age was used to correct mass for size differences; thus, chick mass may reflect faster growth and/or better body condition. Natal dispersal distance was defined as the distance (km; measured between GPS coordinates in Google Earth) moved by an individual from its hatching site to its first breeding site (Clobert et al., 2001). Sites were defined according to Fig. 1, not at the individual nest-site territory scale, because we were interested in dispersal among breeding locations (sites separated by >1.5 km of inhospitable shoreline; Saunders et al., 2012) throughout the Great Lakes region, rather than dispersal within sites. Thus, any dispersal event <2 km was considered philopatric (i.e., 0 km). Prior to analysis, natal dispersal distance was $\log_{10}(x + 1)$-transformed because the distribution of original values was skewed. Including the value 1 in the transformation accounted for dispersal distances of 0 km and improved model fit compared to the standard log-*x* transformation (Pasinelli et al., 2004). Timing of breeding was defined as the Julian date (where 1 = 1 June) on which a female's first nest of the season hatched or was predicted to have hatched, if lost during incubation. Because monitoring does not begin simultaneously at all nesting sites within the Great Lakes region, arrival dates were not available as a measure of timing of breeding. Thus, hatch dates of first nests were used as an index of breeding time. Timing of breeding was considered a female trait, but because males could influence breeding

time due to earlier arrival than females to secure and defend territories (Haig and Oring, 1988), we examined the effect of the male on variation in timing of breeding by including male identity as an additional random effect in the analysis (see below; Husby et al., 2012).

Our pedigree was derived from field observations of 3193 individuals over four generations. While there is evidence for extra-pair paternity in some shorebirds (Colwell, 2010), piping plovers exhibit biparental care (i.e., both mates are responsible for incubation and are thus closely tied to the nest site) and polyandry has rarely been documented (Gratto-Trevor and Abbott, 2011). Further, documented polyandry has been sequential, not simultaneous, and has not been recorded in the Great Lakes population (eastern Canadian piping plovers; Amirault et al., 2004). In the Great Lakes region, breeding pairs are fairly patchily distributed (see Fig. 1), often with only a single pair present for at least several dozen kilometers. Most breeding sites have been monitored on a near-daily basis in the last 10 years and only three suspected cases of extra-pair copulations have been reported (S. Saunders, unpubl. data). Moreover, in a closely related species (Kentish plover, *Charadrius alexandrinus*), only low extra-pair paternity rates have been demonstrated (Küpper et al., 2004). Moreover, simulations have shown that rates of paternity errors approximating 5–20% induce little bias on heritability estimation (Morrissey et al., 2007; Charmantier et al., 2011).

For each trait's analysis, non-informative individuals (i.e., birds without phenotypic data) that were not responsible for a pedigree link between two individuals with phenotypic data were removed from the pedigree using the prunePed function in the R package MCMCglmm (Hadfield, 2010). Summary statistics for each of the three

pruned pedigrees used in analyses are provided in Appendix 1 (Table A1). Pedigree statistics are not comparable across analyses because they differ according to available phenotypic data for the particular trait analyzed.

Data analysis: Bayesian animal models.—We used animal models (Kruuk, 2004) to partition the phenotypic variance in chick mass, natal dispersal distance, and timing of breeding into genetic and environmental components of variance. An animal model is a mixed model that explicitly takes into account the resemblance between each individual and all its relatives to estimate the additive genetic variance (V_A). In addition to the random additive genetic effect, an individual's phenotype can be modeled as a function of a number of other random and fixed effects. Thus, an animal model allows for the full exploitation of all pedigree data and simultaneously accounts for several potentially confounding environmental effects (Kruuk, 2004; Postma and Charmantier, 2007). To provide a flexible framework for fitting animal models (O'Hara et al., 2008), we used Bayesian Markov chain Monte Carlo (MCMC) techniques implemented in program R version 3.0.2 with the package MCMCglmm (Hadfield, 2010). The Bayesian approach produces the joint probability distribution of all model unknowns conditional on the observed data. The advantage of this method is that the results obtained are not point estimates, but the whole posterior distributions of fixed and random parameters (Teplitsky et al., 2011). The joint posterior distribution of all parameters was obtained by MCMC sampling. Convergence of MCMC sampling was assessed via the Heidelberg stationarity test and visual inspection of chains (de Villemereuil, 2012).

In addition to estimating V_A, we also included the following as potential random effects when evaluating chick mass (modeled using a normal distribution): hatch year

(V_{HYEAR}) to account for variation due to annual fluctuations in food availability and other factors; hatch site (V_{HSITE}) to account for differences in site quality for chick growth (e.g., temperature, predator communities, food abundances); maternal identity ($V_{MATERNAL}$) to account for common maternal environment effects associated with siblings sharing the same maternal care (e.g., egg and/or rearing environment; Kruuk and Hadfield, 2007); and paternal identity ($V_{PATERNAL}$) to account for common paternal environment effects associated with siblings sharing the same paternal care (males typically raise offspring alone for approximately two weeks after females depart on autumn migration; Cairns, 1982). Standardized hatching date (*SHDATE*; Saunders et al., 2014) was included as a fixed effect to take into account seasonal declines in chick survival (Brudney et al., 2013), possibly due to poorer condition as the season progresses.

For modeling natal dispersal distance (using a normal distribution after transformation), we included the same aforementioned random effects as well as first breeding site (V_{FBSITE}) to account for possible differences in site quality for breeding. A fixed effect of sex (*SEX*) was also included to explain potential sex-specific dispersal, as demonstrated in other avian species (Greenwood and Harvey, 1982).

When modeling female timing of breeding (using a normal distribution; Saunders et al., 2012), we included $V_{MATERNAL}$ and $V_{PATERNAL}$, as well as breeding year (V_{BYEAR}), permanent environmental (V_{PE}), and breeding site (V_{BSITE}) effects. V_{BYEAR} accounted for repeated records in different years and differences between years that might influence breeding time, such as ambient temperature. V_{BSITE} accounted for variation due to breeding location (e.g., later breeding in Michigan's upper peninsula due to colder temperatures). Finally, because we had repeated measures of individuals, V_{PE} was

included to model variation associated with the particular environment of the female (i.e., inherent differences between individuals other than those due to additive genetic or maternal/paternal effects; Kruuk, 2004). Because older females are known to breed earlier (Saunders et al., 2012), age (linear and quadratic terms to account for senescence) was included as a fixed effect (*AGE*).

The trace and densities of fixed and random effects and residuals were checked. Any variance component was removed if it explained a small portion (<2%) of the phenotypic variance and did not reduce DIC relative to a model without the effect (Charmantier et al., 2011). Similarly, any fixed effect with a 95% credible interval (CI) that overlapped zero was considered unsupported and was consequently removed from subsequent models (Wilson et al., 2010). Models were compared using the deviance information criterion (DIC; Spiegelhalter et al., 2002); the model with the smallest DIC value was chosen as the best-supported model. Several methods exist to compare models in a Bayesian framework (O'Hara et al., 2008); we used DIC in accordance with Hadfield (2010) and as implemented in MCMCglmm.

Chick mass models were run with uninformative inverse gamma priors (variance priors set to 1, degree of belief [*n*] of 0.002), which is typical for MCMCglmm (Wilson et al., 2010); estimates were similar for different priors tested. Priors for natal dispersal distance and timing of breeding models used parameter expansion to avoid poor mixing if variance component estimates were close to zero (Postma et al., 2011). All models were run for 1,000,000 iterations, preceded by a burn-in of 50,000 iterations. Estimates of every 100th iteration were stored to reduce the autocorrelation among subsequent

iterations. These designations resulted in effective sample sizes of 7,000–10,000 for all random effects in all analyses.

The heritability (h^2) of each trait was calculated as the proportion of phenotypic variance (V_p) that had an additive genetic basis, where V_p was the sum of variance components from the top-supported model according to DIC. Repeatability (V_I) of breeding time in females was calculated as the proportion of V_p explained by the individual (i.e., $V_A + V_{PE}$; Wilson et al., 2010). 'Evolvability' was measured as the coefficient of additive genetic variation: $CV_A = V_A^{0.5}/\text{mean} \times 100$, where mean is the trait's population mean (Houle, 1992; Husby et al., 2012). Means, variance components, and heritabilities are presented as ±1 standard error (SE) unless otherwise noted.

RESULTS

Mean chick mass (controlled for age at banding: log(mass [g]) = 2.02 + 0.09 × age; n = 1401 individuals) was 0.009 ± 0.007; this was equivalent to a mean mass of approximately 12.5 g at 6 days of age. A low residual mass score (i.e., smaller than average chick) of -0.40 corresponded to approx. 5.4 g lighter at 9 d of age and a high residual mass score (i.e., heavier than average chick) of 0.33 corresponded to approx. 6.4 g heavier at 9 d of age, for example. Median natal dispersal distance (raw data; n = 295 individuals) was 79.6 ± 4.6 km (interquartile range: 82.5 km); maximum dispersal distance was 463 km. Mean Julian date (1 = 1 June) of female breeding time was 17.0 ± 0.6 (17 June; n = 303 records; n = 92 unique females).

There was a significant additive genetic component to phenotypic variance in residual chick mass (Table 1), resulting in a heritability of 0.27 (95% CI: 0.16–0.38) and a relatively high evolvability of CV_A = 13.82. The best-supported model included

significant effects of hatch year, common maternal environment, and hatch site (Table 1). Paternal common environment effects were small and non-significant (explaining <2% of variation), and were therefore not included in the top model. Additionally, the fixed effect of standardized hatch date was not supported (*SHDATE* = 0.0123; 95% CI: -0.0038–0.0257). Overall, genetic effects accounted for 27% of the variation in chick mass, and the combined environmental effects of hatch year, maternal common environment, and hatch site explained 43% of the variation, with residual variation accounting for the remaining 29% (Fig. 2A). Hatch year effects indicated that chicks were lighter than average during 1995–1996, 2010, and 2012; chicks were heavier than average during 2001–2003 and 2006–2007 (Fig. 3A). On average, chicks hatching at Cathead Bay, Pointe aux Chenes area, Beaver/High Islands, Port Inland, and Wilderness State Park were heavier, whereas chicks hatching at Grand Marais, Ludington/Manistee, Whitefish Point, Vermilion, and Sleeping Bear Dunes were lighter (Fig. 3B).

The additive genetic component of natal dispersal distance was low; consequently, estimated heritability (h^2 = 0.03; 95% CI: 0.0–0.11) and evolvability (CV_A = 0.02) were very low, indicating that environmental factors were the main sources of variation in dispersal distance. The best-supported model included effects of first breeding site, hatch site, maternal common environment, and paternal common environment (Table 1). The hatch year effect explained an insignificant portion (<2%) of the variation in natal dispersal distance. We did not find support for sex-specific dispersal (*SEX* = 0.02; 95% CI: -0.135 to 0.167). Combined site effects (hatching and first breeding) accounted for the largest proportion of phenotypic variation (38%) other than residual variance, and combined maternal and paternal common environment effects

explained another 5% of the variation (Fig. 2B). Birds that hatched at Grand Marais dispersed shorter distances, on average, to sites of first breeding. Birds that first bred at Wilderness State Park, North Manitou Island, Grand Marais, and Sleeping Bear Dunes dispersed shorter distances than average from their hatch locations, whereas birds that bred at Long Island (Wisconsin, USA) dispersed longer distances than average (Fig. 4).

The additive genetic component of female timing of breeding was low; thus, estimated heritability (h^2 = 0.08; 95% CI: 0.0–0.22) and evolvability (CV_A = 1.69) were also low. The best-supported model included breeding site, mate, and permanent environmental effects (Table 1). Repeatability of breeding time was significant (V_I = 0.16; 95% CI: 0.04–0.29), indicating that variation among females contributes approximately 16% to the total variation in breeding time. Common maternal and paternal environment, as well as breeding year effects explained insignificant portions of the phenotypic variance (<2%). The fixed effect of age (linear and quadratic terms) on female breeding time was strongly supported (*AGE* = -6.86, 95% CI: -8.29 to -5.71; AGE^2 = 0.50, 95% CI: 0.37–0.63). With the exception of residual variance, breeding site accounted for the largest proportion of phenotypic variance (33%; Fig. 2C). The influence of the male on variation in female breeding time was supported, but only accounted for 5% of the variation (Fig. 2C). Breeding site effects indicated that females bred earlier than average at Sleeping Bear Dunes and North Manitou Island, whereas females bred later than average at Long Island, Indian Point, and Whitefish Point (Fig. 5).

DISCUSSION

A previous analysis of this same plover population demonstrated the importance of age-corrected chick mass in predicting pre-fledging survival (Saunders et al., 2014).

Therefore, understanding the contributors to variation in this trait was of particular interest. Our results indicate a significant additive genetic variance in piping plover chick mass, indicating that non-skeletal body weight in piping plovers is not solely a reflection of an individual's nutritional, and hence non-genetic, state. Similarly, recent studies have demonstrated a significant additive genetic component of phenotypic variation in offspring body weight for passerine species (blue tit, Merilä et al., 1999; collared flycatcher, Merilä, 1996 and Merilä et al., 2001). However, our metric may represent differential growth (i.e., bigger structural size) and/or differences in condition. Similarly, other studies have found a heritable component to growth in various avian species, including great tits (Parus major; Noordwijk et al., 1988) and willow tits (*Parus montanus*; Thessing and Ekman, 1994).

We found substantial non-genetic contributions to variation in chick mass as well, including a common maternal environment effect, suggesting that the mother's phenotype affects the phenotype of her offspring in ways additional to the additive effects of the genes she has passed on. This component of variance could arise through several mechanisms, including: (1) differences in maternal investment in eggs; or (2) differences in parental care during the first few weeks of chick growth (Kruuk and Hadfield, 2007). Egg measurements are unavailable for this population, but a previous study investigated the influence of parental experience on reproductive success and demonstrated that female site familiarity increased fledging success (Saunders et al., 2012). Thus, we posit that a female's site-specific knowledge (e.g., high-quality foraging areas) may be contributing to the maternal effect on offspring mass, given its known influence on fledging success (i.e., chick survival). This assertion is further supported by a significant

environmental influence of hatch site on chick mass. Differences in average ambient temperature and precipitation among sites can affect insect prey availability (LeFer et al., 2008; Catlin et al., 2012) and the amount of time young chicks spend being brooded instead of foraging (Schekkerman and Visser, 2001), contributing to site-specific variation in mass. Specifically, chicks hatching at all Lake Superior sites were lighter than average, and these sites are also colder (comparing daily low temperatures) than average with colder water temperatures, compared to Lake Michigan locations (Brudney et al., 2013). Finally, annual fluctuations in prey abundances may partly explain the considerable temporal variability in chick mass, with hatch year effects accounting for approximately 12% of the variation in this trait.

We found very low heritability and evolvability of natal dispersal distance in piping plovers. The phenotypic variance was largely due to variation between hatching and first breeding sites as well as unexplained (residual) variance. The large residual variance may be due to unmeasured social factors, including variation in overwintering locations of individuals that may influence arrival locations on the breeding grounds and/or variation in local reproductive success among breeding sites that may influence dispersal decisions (Rioux et al., 2011). Gene-by-environment interactions also contribute to residual variance, but are difficult to assess in natural populations, as opposed to lab studies or breeding programs. Site (hatch and first breeding) effects explained a substantial portion of the variation in dispersal distance, and this was likely a consequence of habitat quality differences among locations. For example, Sleeping Bear Dunes and North Manitou Island are typically sites with high reproductive success, which may explain why birds that first bred at those locations dispersed shorter distances from

their hatch locations. Making dispersal decisions based on personal and public information, such as preferentially choosing sites where breeding success is high, has been demonstrated in a piping plover population breeding in eastern Canada (Rioux et al., 2011). Thus, as previously suggested (Pasinelli et al., 2004; Charmantier et al., 2011), dispersal can be considered a plastic response to a set of biotic and abiotic conditions rather than thought of as a fixed dispersal distance. Future studies should consider relating natal and breeding dispersal, both phenotypically and genetically, once additional data on breeding conditions for related and unrelated individuals are obtained. Because site effects were important in explaining variation in both natal dispersal and female breeding time (see below), any management actions to maintain or enhance piping plover nest site quality and suitability (e.g., phragmites [*Phragmites australis*] removal, prevention of beach grooming) may help stabilize population dynamics in the face of ongoing climate change.

The additive genetic variance component of female timing of breeding was small, and consequently, heritability and evolvability estimates of the trait were low. While a substantial portion of the phenotypic variance remained unexplained, breeding site effects did account for a large (33%) portion. Consistent with our expectations, females bred earlier at sites further south in Michigan's lower peninsula (e.g., Sleeping Bear Dunes) and later at sites in the upper peninsula (e.g., Whitefish Point) and Wisconsin, where temperatures are cooler earlier in the season. Mate effects influenced female breeding time to a small degree; variation in timing of male arrival on the breeding grounds, which occurs prior to female arrival, likely contributes to this effect. Stronger mate effects on female breeding time have been found in red-billed gulls (*Larus novaehollandiae*

scopulinus; Teplitsky et al., 2010) and common terns (*Sterna hirundo*; Nisbet, 1973), but these are species in which females highly depend on males to provide their energetic requirements during incubation (i.e., courtship feeding), which is not the case in piping plovers. We found significant between-female variance in breeding time, even after correcting for age. Thus, intrinsic differences in the breeding histories of individuals are partly driving variation in breeding time in this population.

Natal dispersal and timing of breeding in piping plovers are strongly influenced by environmental variation. The low potential for these two traits to evolve in response to natural selection may limit the ability of the population to adapt to environmental change in the long-term. Due to declining water levels, more shoreline habitat may temporarily become available for nesting plovers, but some breeding sites are also expected to become less favorable in the near future given changing shoreline conditions in the Great Lakes as a result of climate change (Angel and Kunkel, 2010). Additionally, optimal breeding time may shift given fluctuations in insect prey abundances with climate (i.e., 'phenological mismatch'; Reed et al., 2013). Predation risk during migration can also dictate ideal breeding time (Charmantier and Gienapp, 2014); for shorebirds, timing of migration partly depends on risk of predation by birds of prey (e.g., Lank and Ydenberg, 2003). If quality of piping plover breeding areas, prey availability, or migration timing is adversely affected by environmental changes, evolution towards higher natal dispersal or earlier breeding time could be necessary for this population's long-term persistence (Charmantier et al., 2011), depending on whether such environmental changes reduce the population growth rate below replacement.

The low heritabilities of these two traits suggest that such a microevolutionary process would not be feasible, but rather alterations in dispersal and breeding time could change primarily by a phenotypically plastic response. Phenotypic plasticity could permit a rapid adjustment to novel environmental conditions and allow a population to persist in the short-term, until evolutionary adaptation can occur (Chevin et al., 2010; Kovach-Orr and Fussmann, 2013). Consequently, phenotypic plasticity may be considered a better strategy to cope with environmental change, such as global climate change, as it can allow for faster tracking of a changing environment (Charmantier and Gienapp, 2014). Thus, flexibility of natal dispersal and timing of breeding in piping plovers may be beneficial as it can 'allow' for tracking of annual fluctuations in the environment that may impact breeding sites and/or food availability. However, for plasticity to remain efficient during an environmental change, the relationship between the environment that determines the trait (i.e., the 'cue') and the environment that determines fitness (i.e., the 'selective environment') must remain the same during the selective process, which may not necessarily be the case under continued climate change (Charmantier and Gienapp, 2014). For example, great tits time their breeding according to temperatures (i.e., 'cues') in early spring. Yet their reproductive success depends on the occurrence of caterpillars later in the season, and caterpillar phenology is determined by temperatures in late spring (Visser, 2008). In the Netherlands, a differential change in these spring temperatures has altered the relationship between the 'cue' and the optimum phenotype (Nussey et al., 2005). To our knowledge, this is the first time that the genetic basis of any phenotypic trait other than egg size (female repeatability; Väisänen et al., 1972) has been examined in a wild shorebird population. It would be interesting to determine if the minimal genetic

influences (and considerable environmental influences) on natal dispersal and breeding time reported here are exhibited in other shorebird species, some of which demonstrate considerable vagility (Stenzel et al., 2007).

CONCLUSIONS

The measurement of genetic variation is an important component of many endangered species management programs, as a decline in genetic variation can preclude a population's ability to respond to natural selection and consequently limit its evolutionary potential (Storfer, 1996). Because endangered populations often are carefully censused and measurements of life-history and morphological traits are already collected by researchers, the application of quantitative genetic techniques is feasible. Results from such studies can help identify management priorities, depending on the relative contribution of genetic and environmental influences on the trait of interest. In this study, site effects significantly contributed to variation in both natal dispersal and female breeding time, emphasizing the need to maintain and enhance nesting site suitability, especially given predicted changes in Great Lakes water levels due to climate change. Given the negative relationship between breeding time and offspring survival in this population (pre-fledging survival, Brudney et al., 2013; first-year survival, Saunders et al., 2014), such management actions may lead to increased recruitment. Importantly, this analysis demonstrates that genetic control is not strongly inhibiting alterations in dispersal distance and breeding time in Great Lakes piping plovers, leading to a greater flexibility in facing climate change.

Additionally, endangered species management and recovery plans often involve captive breeding and release of individuals into areas where they were once extant, or

translocations of individuals into new areas. Knowledge of how these organisms may respond to changes in environmental conditions can be critical for the success of such programs (Lande and Shannon, 1996). Estimates of heritabilities for pertinent traits will allow managers to assess the potential for response to selection. For example, if the heritability of an organism's response to heat stress is extremely low in a population occurring where the temperature is predicted to rise several degrees, mixing of populations can potentially increase additive genetic variation, and thus increase the overall population's ability to respond to warmer temperatures.

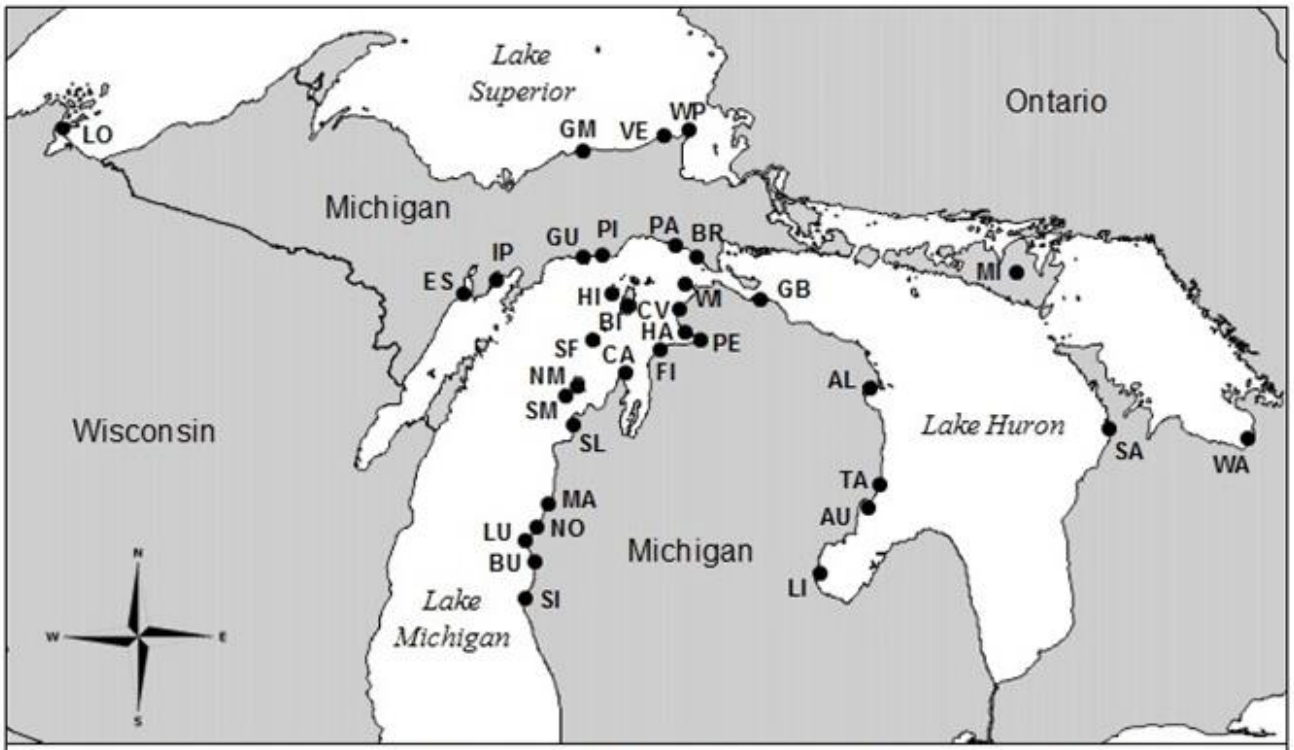
In addition to increased temperatures, global climate change is resulting in more frequent extreme climatic events (Rummukainen, 2012). It is possible that adaptation could proceed mainly due to a heritable change in individual reaction norms (e.g., fine-tuned adjustments in phenology), rather than in the phenotype averaged over environments (Charmantier and Gienapp, 2014). Studying variation in plasticity of life-history and phonological traits adds statistical complexity and requires large datasets with repeated measures on individuals, but such investigations will greatly advance our knowledge of how bird populations can adapt to increasing weather variability. Finally, very few studies have attempted to gauge the demographic consequences of adaptation (or non-adaptation) in wild bird populations (but see Reed et al., 2013; Vedder et al., 2013); none have been conducted regarding an endangered population. Future studies should fill this knowledge gap by using results from quantitative genetic analyses, such as this one, to predict possible effects of climate change on dynamics and persistence of populations, particularly for those that are already threatened or endangered.

TABLE 1. Variance components that determine chick mass (age-corrected), natal dispersal distance, and female timing of breeding in Great Lakes piping plovers (1994–2013), according to top-supported Bayesian animal models. V_P = phenotypic variance; V_A = additive genetic variance; V_R = residual variance; and variances due to the following effects: hatch year (V_{HYEAR}), maternal common environment ($V_{MATERNAL}$), paternal common environment ($V_{PATERNAL}$), hatch site (V_{HSITE}), first breeding site (V_{FBSITE}), breeding site (V_{BSITE}), mate (V_{MATE}), and permanent environmental (V_{PE}).

Parameter	**Estimate**	**95% credible interval**
Chick Mass		
V_P[a]	0.0707	-
V_A	0.0191	0.01-0.03
V_{HYEAR}	0.0078	0.00-0.02
$V_{MATERNAL}$	0.0154	0.01-0.02
V_{HSITE}	0.0057	0.00-0.02
V_R	0.0227	0.02-0.03
Natal Dispersal Distance		
V_P[b]	0.4653	-
V_A	0.0004	0.00-0.06
V_{HSITE}	0.0435	0.00-0.27
V_{FBSITE}	0.1125	0.03-0.28
$V_{MATERNAL}$	0.0002	0.00-0.04
$V_{PATERNAL}$	0.0001	0.00-0.05
V_R	0.3086	0.25-0.38
Female Timing of Breeding		
V_P[c]	63.206	-
V_A	0.0867	0.00-20.92
V_{BSITE}	19.907	6.31-76.21
V_{MATE}	0.0421	0.00-13.23
$V_{PERMENV}$	0.1323	0.00-19.65
V_R	43.038	34.4-53.90

[a] $V_P = V_A+V_{HYEAR}+V_{MATERNAL}+V_{HSITE}+V_R$
[b] $V_P = V_A+V_{HSITE}+V_{FBSITE}+V_{MATERNAL}+V_{PATERNAL}+V_R$
[c] $V_P = V_A+V_{BSITE}+V_{MATE}+V_{PERMENV}+V_R$

FIGURE 1. Distribution of major piping plover nesting locations in the Great Lakes region during 1994–2013. Our analysis utilized data from all sites shown.



AL-Alpena; **AU**-Au Sable; **BI**-Beaver Is.; **BR**-Brevort; **BU**-Buttersville; **CA**-Cathead Bay; **CV**-Cross Village; **ES**-Escanaba; **FI**-Fisherman's Is.; **GB**-Grass Bay; **GM**-Grand Marais; **GU**-Gulliver; **HA**-Harbor Springs; **HI**-High Is.; **IP**-Indian Point; **LI**-Linwood; **LO**-Long Is.; **LU**-Ludington; **MA**-Manistee; **MI**-Manitoulin Is.; **NM**-North Manitou Is.; **NO**-Nordhouse Dunes; **PA**-Pointe aux Chenes; **PE**-Petoskey State Park; **PI**-Port Inland; **SA**-Sauble Beach; **SI**-Silver Lake; **SF**-South Fox Is.; **SL**-Sleeping Bear Dunes; **SM**-South Manitou Is.; **TA**-Tawas Point State Park; **VE**-Vermilion; **WA**-Wasaga; **WI**-Wilderness State Park; **WP**-Whitefish Point

FIGURE 2. Causal components of phenotypic variance in chick mass (A), natal dispersal distance (B), and female timing of breeding (C) of Great Lakes piping plovers from the top-supported Bayesian animal models. h^2 = heritability; see Table 1 for variance component abbreviations. Bars represent ± 1 standard error.

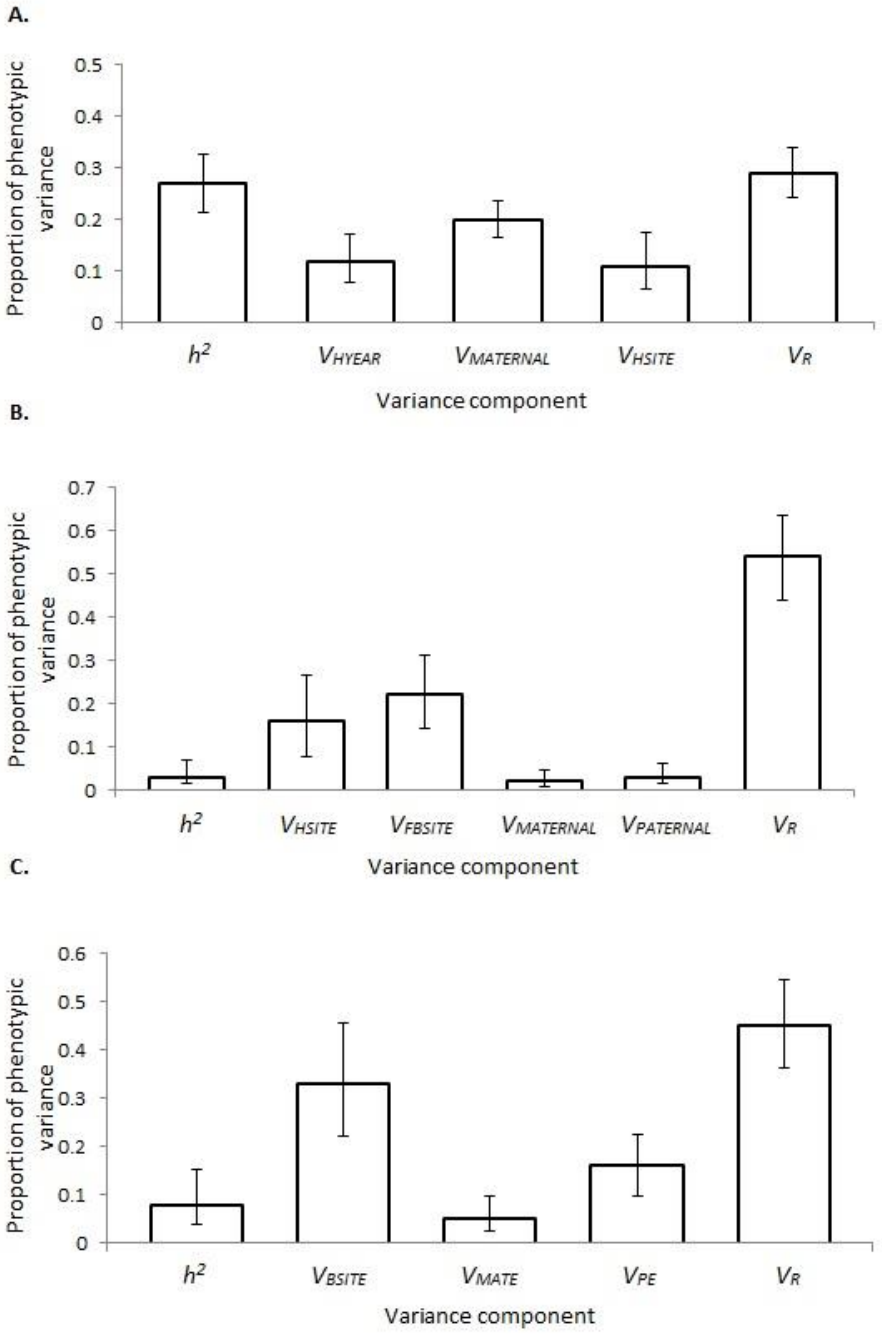


FIGURE 3. Prediction intervals of the hatch year effect (A) and hatch site effect (B) on chick mass. Hatch years (A) and sites (B) are listed on the *y*-axes and their influences (either positive or negative) on chick mass are shown along the *x*-axes. See Results for interpretation of which hatch years and hatch sites were associated with chicks that were lighter and heavier than average. Site abbreviations are listed in Fig. 1.

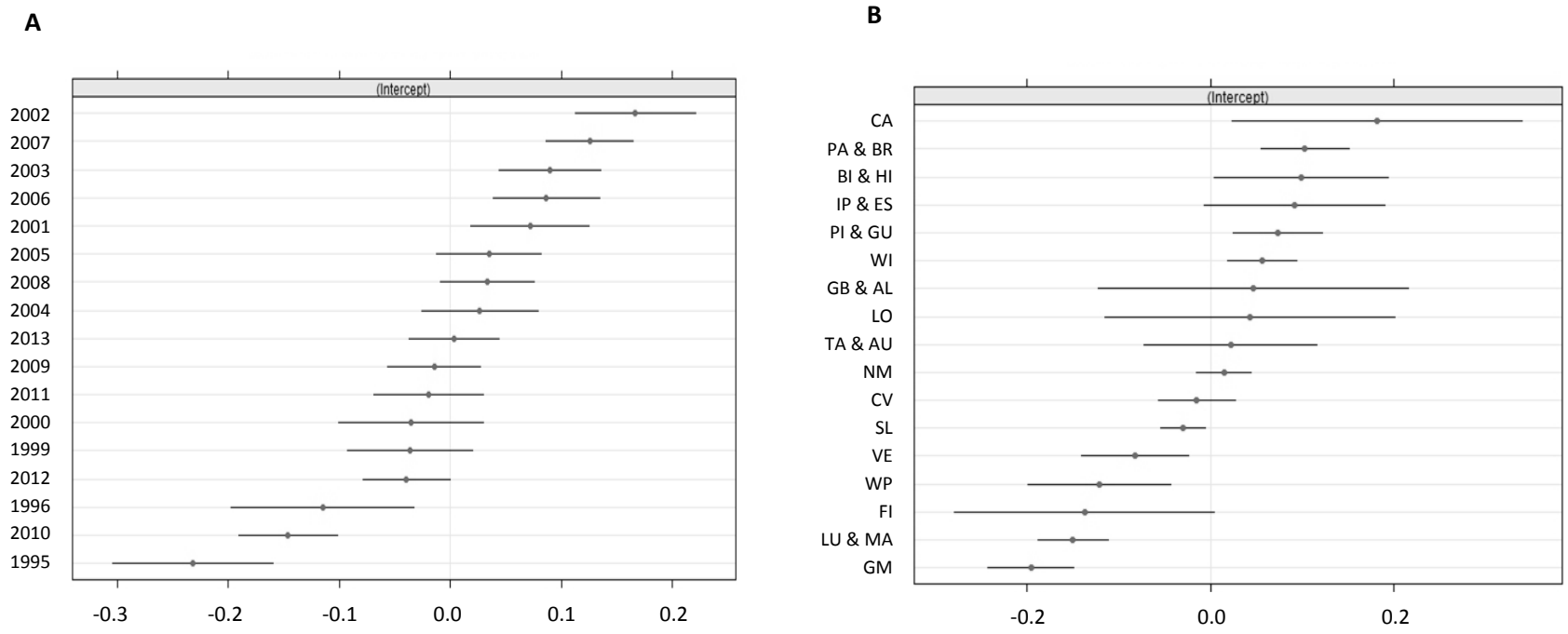


FIGURE 4. Prediction intervals of the first breeding site effect on natal dispersal distance. Sites are listed on the *y*-axis and their influence (either positive or negative) on dispersal distance is shown along the *x*-axis. Sites with intervals that do not overlap zero had a significant influence on natal dispersal distance.

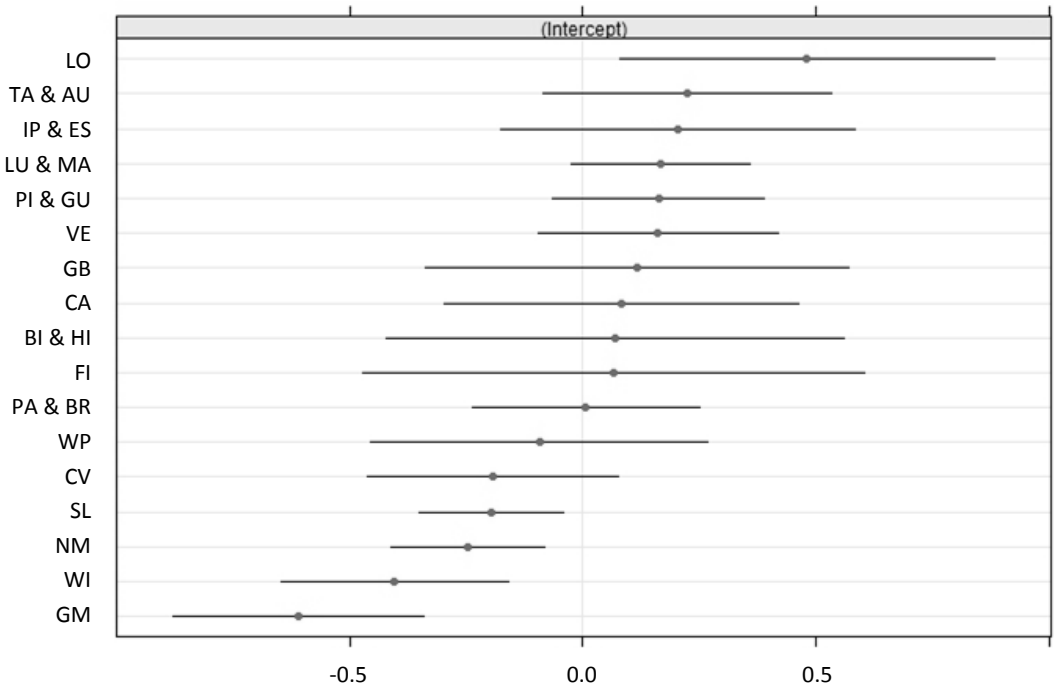
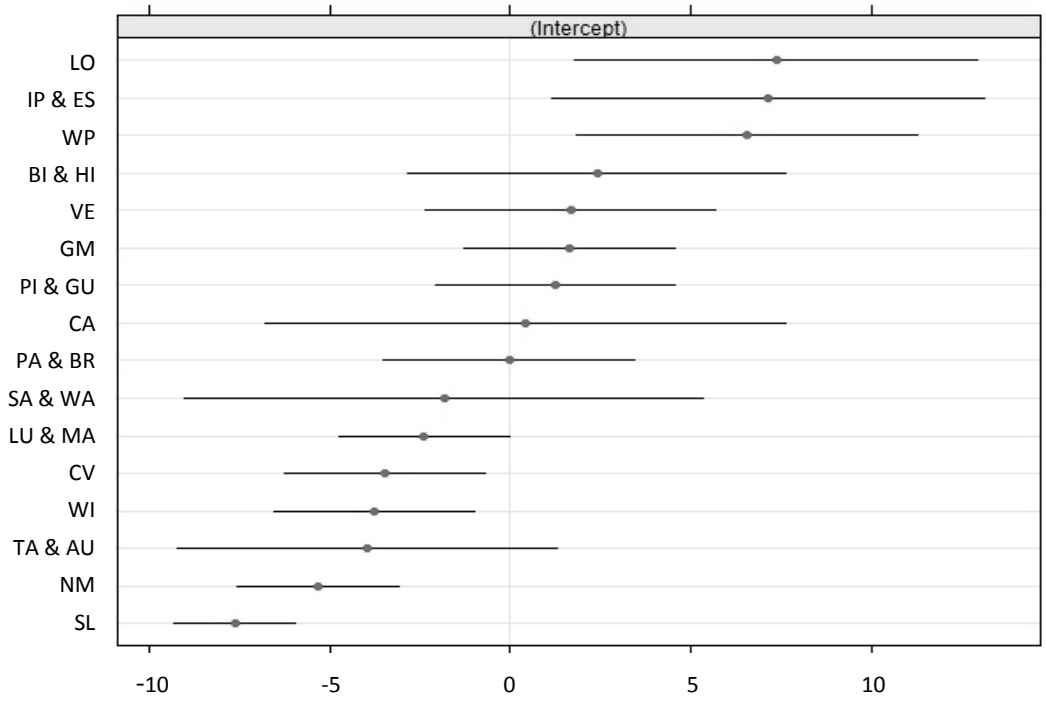


FIGURE 5. Prediction intervals of the breeding site effect on female timing of breeding. Sites are listed on the *y*-axis and their influence (either positive or negative) on breeding time is shown along the *x*-axis. Sites with intervals that do not overlap zero had a significant influence on breeding time.



CHAPTER 3

AGE-SPECIFIC SURVIVAL AND RECRUITMENT OF PIPING PLOVERS (*CHARADRIUS MELODUS*) IN THE GREAT LAKES REGION

THE PROBABILITY THAT offspring born into a population will ultimately enter the population as breeding adults is determined by survival through the pre-breeding period and recruitment into the breeding population after reaching sexual maturity (Plissner and Haig 2000, Cam et al. 2005, Hadley et al. 2007, Mullin et al. 2010). Understanding these processes is especially critical for threatened species, where effective conservation strategies depend on accurate assessments of population trajectories and the most effective places to intervene (Sandercock et al. 2005). Many studies have examined the effect of adult survivorship on avian population dynamics (Sæther and Bakke 2000), but comparatively few have investigated juvenile survivorship and recruitment due to difficulties in following offspring after they leave the nest or brood-rearing areas. There is also pronounced natal dispersal in many species (Greenwood and Harvey 1982), and because the complement of apparent survival in capture-mark-recapture studies includes mortality and permanent emigration (Schaub and Royle 2013), juvenile survival estimates are more prone to bias from permanent emigration. Additionally, knowledge of age-specific recruitment in many birds is based on distributions of age at first capture, which inaccurately assumes that detection probability of first-time breeders is perfect (Sandercock 2003).

Juvenile survival (i.e. survival during the first year of life) is negatively correlated with hatch date in many species, either due to earlier nesting by higher-quality parents (Lepage et al. 1999, Saunders et al. 2012) or declining environmental conditions over the course of the breeding season (Ruthrauff and McCaffery 2005, Paasivaara and Pöysä 2007). Furthermore, previous studies have demonstrated substantial spatial variation in survival of young (Colwell et al. 2007, Le Fer et al. 2008), perhaps due to differences

among breeding locations, such as temperature (Brudney et al. 2013) or human disturbance (Ruhlen et al. 2003). Offspring quality, as reflected by body condition, has also been shown to influence pre- and post-fledging survival in numerous bird species (Magrath 1991, Naef-Daenzer et al. 2001, Dinsmore et al. 2003). Additional variation in juvenile survival can be associated with variation in predator abundances, weather patterns, food availability, or other unknown environmental factors (Guyn and Clark 1999). For example, while extreme temperatures and inclement weather may have a direct impact on survival of pre-fledged offspring (Harris et al. 2005, Brudney et al. 2013), low temperatures might also decrease insect prey abundances and affect post-fledging and overwintering survival, especially among naïve chicks with limited foraging experience (Evans 1976, Le Fer et al. 2008).

The age at which an individual transitions from pre-breeder to breeder can have an important effect on lifetime reproductive success (Spendelow et al. 2002). Age at first breeding may be influenced by several factors, including natal conditions, reproductive maturity, timing of migration, and knowledge of food and habitat availability at breeding sites (Braby et al. 2011). We hypothesized that early hatching date and enhanced body condition at fledging may play important roles in recruitment probability because such individuals would likely have better foraging skills, earlier migration, better access to high quality wintering sites, and return earlier to breed (Spear and Nur 1994, Verboven and Visser 1998, Dawson and Clark 2000, Guillemain et al. 2013).

The piping plover (*Charadrius melodus*) is a migratory shorebird endemic to North America, breeding in the Great Plains, Great Lakes and Atlantic Coast and wintering from the southern Gulf of Mexico to the southern U.S. Atlantic Coast. The

Great Lakes population of piping plovers is an ideal study population to address questions of survival and recruitment because individuals of known ages have been marked and resighted since 1993, allowing us to explore the potential effects of annual and individual covariates that might affect survival and recruitment probabilities during both the juvenile and adult stages. Additionally, resighting probability of breeding adults is near perfect (LeDee et al. 2010), indicating that individuals who return to breed will likely be encountered. Finally, because monitoring occurs throughout the entire known breeding range, young are likely to be encountered even if they disperse to a new breeding location within the Great Lakes. Because of their status as a federally threatened species, piping plovers have been intensively monitored in all three recognized populations, and only one color-marked plover has ever been documented as emigrating from the Great Lakes population (Hillman et al. 2012).

We used a long-term (1993–2012) capture-mark-recapture data set to examine factors affecting piping plover survival and recruitment in the Great Lakes region. Our objectives were to: 1) estimate survival of first-year and adult piping plovers, 2) estimate age-specific probability of first breeding, and 3) assess the importance of individual-, year-, and site-specific covariates on survival and age at first reproduction. Results from this analysis will help improve our understanding of how management can be enhanced to increase survival and recruitment in this endangered population.

METHODS

Focal species and study area.— The federally endangered Great Lakes population of piping plovers nests on wide, sparsely vegetated sand and cobble beaches along the shoreline of lakes Michigan, Superior and Huron (U.S. Fish and Wildlife Service

[USFWS] 2003), and winters primarily along the U.S. Atlantic coastline ranging from North Carolina to Florida and the Bahamas (Stucker et al. 2010). Since 1986 (USFWS 1985), the population has fluctuated between 17 and 71 known breeding pairs (Cuthbert and Saunders, unpubl. data). Females typically produce a four-egg clutch, and both parents incubate and assist in rearing precocial young. Nests are protected by wire exclosures to reduce egg predation (Melvin et al. 1992) and recreational activities are managed to reduce human disturbance in breeding areas (USFWS 2003). Our study used data from all known nesting locations during 1993–2012 (see Chapter 2: fig. 1).

Field data collection.— Surveys were conducted at historical, recent, and potential nesting habitats to locate breeding pairs. Breeding pairs were monitored every one to four days from nest initiation until all chicks disappeared or fledged. Plovers were banded using U.S. Geological Survey (USGS) aluminum bands and Darvic color bands (Avinet, Dryden, NY, USA). Adults received unique color combinations, whereas chicks received brood-specific color combinations that did not allow for individual identification without recapture. Unmarked or brood-marked (i.e. previously marked as chicks) incubating adults were trapped on the nest (Lincoln 1947) and given individual-specific color combinations; chicks were caught by hand. First-year survival was defined as the period from banding (5–15 d old; median banding date = 1 July) to the median trapping date for nesting birds (9 June). In a post-hoc analysis where chicks that died prior to banding were excluded, first-year survival was defined as the period from fledging (23 d old) to the median trapping date for nesting birds. Recruitment was defined as the age at which an individual was first observed nesting (i.e. age at first reproduction).

Data summary.— We used data from 1826 individuals first banded as chicks

(*n* = 1706) or adults (*n* = 120) during 1993–2012, excluding captive-reared individuals (Roche et al. 2008). We compiled multi-state, 20-occasion encounter histories for individual birds from year of hatch through 2012. Encounters were coded as either '0' (bird not yet marked or not observed that year), or as one of three states: 'P' (marked as a juvenile/pre-breeder of unknown sex), 'M' (captured/observed as a breeding male), or 'F' (captured/observed as a breeding female). In capture histories, birds transitioned from state P to state M or F (i.e. transitioned from pre-breeder of unknown sex to breeding male or female) when they were first captured on a nest, sexed, and given a full complement of adult bands. However, they may have transitioned to a breeder but avoided capture in earlier years. Birds were sexed using observations of the bird's position during copulation or other sex-specific behaviors exhibited prior to nesting (e.g. nest scraping by males). We treated states M and F as absorbing states; individuals seen alive on the breeding grounds in future years (i.e. after they had already nested once and received a full color combination) were coded as alive in state M or F, whether or not they were observed nesting. Thus, a capture history spanning 1993–2012 such as 0000P00FFFFFFF000000 would represent a chick first marked in 1997, captured as a breeding female in 2000 and seen every subsequent year through 2006. Apparent survival estimates from our multi-state models approximate true survival given nearly complete monitoring of this closed population. However, LeDee et al. (2010) found a slight discrepancy (7%) between true and apparent survival estimates, indicating that not all birds return to the study area.

Individual covariates.— We included hatching date (HDate; 1 June = 1) as an individual covariate on first-year survival and age at first reproduction. Because nesting

chronology varied annually, we also considered standardized hatching date (StdHDate) by subtracting the annual mean and dividing by the annual standard deviation. Both variables performed similarly, but StdHDate was better supported by AIC_c than was HDate, so hereafter we only report results based on StdHDate. We included age at banding (BandAge = 0 at hatching) as a covariate on first-year survival because chicks banded at younger ages were less likely to survive through their first year (Roche et al. 2008, Brudney et al. 2013). We used residuals from a regression of $\log_e$-body mass on age at banding (to control for differences in body size with age, Condition; Schulte-Hostedde et al. 2005) as a covariate on both first-year survival and age at first reproduction. Individuals that were not weighed (n = 239; 14% of individuals) were assigned a residual condition value of 0 (Cooch and White 2012).

Temporal covariates.— We included annual covariates on merlin abundance, minimum temperatures on the breeding and wintering grounds, and hurricane frequency on the wintering grounds as potential correlates of annual survival for both juvenile and adult plovers. Merlins are an important predator of breeding and wintering plovers (Neuman et al. 2004, Roche et al. 2010b). To index their annual abundance, we applied state space models (Kéry and Schaub 2012) to raw annual counts of merlins migrating through Hawk Mountain, Pennsylvania during autumn (Aug–Dec; www.hawkmountain.org) and through Whitefish Point in Michigan during spring (March–May; www.wpbo.org). We used estimates from Whitefish Point to index merlin abundance on the breeding grounds (MerlinSummer) and combined estimates from Whitefish Point and Hawk Mountain to approximate merlin abundance on the non-breeding grounds (MerlinWinter). Migration through Hawk Mountain is thought to be the

primary route of merlins leaving their breeding grounds in the northern United States heading to the southeastern U.S. Atlantic coast and South America (www.hawkmountain.org).

As an indicator of direct mortality due to severe weather (Noel and Chandler 2008) or potential indirect mortality due to storm-induced habitat loss (Johnson and Baldassarre 1988), we tallied the number of hurricanes impacting the southern U.S. Atlantic Coast (North Carolina through Florida) during 15 August–31 December of each year (Hurricane; primary hurricane season is from 1 June–30 November, but plovers do not arrive until mid-August). Cold temperatures can decrease survival during the first few days of life when chicks are unable to thermoregulate effectively (Harris et al. 2005, Brudney et al. 2013), but low temperatures could also affect survival through reduced food availability (Elkins 2010). Thus, we included mean monthly minimum temperatures for the non-breeding and breeding seasons (see 'Spatio-temporal characteristics of breeding sites' for breeding season details) using weather data obtained from the National Climatic Data Center (NCDC). For the non-breeding season, we calculated a mean minimum temperature (NBTemp) from 1 March-30 April at each of three major non-breeding locations used by Great Lakes piping plovers: St Simon's Island, Georgia; Topsail Island, North Carolina; and Deveaux Bank, South Carolina (Stucker et al. 2010). This time period was chosen because a previous analysis of Great Lakes piping plovers demonstrated that seasonal survival was lowest in the spring, but was positively associated with ambient temperatures on the wintering grounds (Roche 2010).

Spatio-temporal covariates.— We included mean minimum temperature (BreedTemp) during 1 June–31 July (peak of hatching and chick growth) measured near

each breeding site and total fledglings produced per breeding site per year (CohortSize) as potential site-specific covariates affecting first-year survival. Temperature data (National Climate Data and Information Archive; www.climate.weatheroffi ce.gc.ca) were obtained from weather monitoring stations located closest to each of the individual nesting locations (see Chapter 2: fig. 1; range: 1 km [CV, ES, GM, LU, MA, WP] to 129 km [Canadian sites], mean distance: 18.8 km). Data from a total of 21 monitoring stations were used. Mean minimum temperatures were calculated at each site for the duration of the chick-rearing period to best approximate the potential influence of cold temperatures on prey availability during chick growth (Lepage et al. 1999, Schekkerman et al. 2003, Catlin et al. 2012).

We reasoned that cohort size might have positive or negative effects on first-year survival (Harris et al. 1994, Spear and Nur 1994). Higher densities of young individuals may attract predators and/or limit food resources, yet interactions with more fledglings may be beneficial for avoiding predators and preparing for autumn migration because the majority of juvenile plovers migrate after adults have departed (Cairns 1982). We defined cohort size as the total number of fledglings present at an individual's nesting location during an individual's hatching year. Although not all chicks at a nesting location fledged during the same period, we did not have accurate historical records on the duration of chick presence post-fledging at each site. Thus, for this analysis, we assumed that the total number of chicks fledged per site was an accurate measure of cohort size for a given individual.

Detection of first-time breeders.—Because chicks were banded with batch markers (i.e. brood-specific combinations), they had to be captured as nesting adults for

positive identification. We therefore included 19 occasion-specific individual covariates, indicating whether an individual was wearing chick or adult bands (ChickBand = 1 or 0, respectively) at the beginning of each breeding season (Appendix 2). All occasion-specific covariates were coded as 1 until the year after an individual received adult bands. For example, the individual occasion-specific covariate vector 1110000000000000000 represents a bird first recaptured in year 3 (1995), and available to be resighted based on adult bands in years 4–20 (1996–2012). We treated state P (pre-breeding) birds with ChickBand = 1 as undetectable because they could not be captured for positive identification until they started nesting. Thus, all state P birds had to transition to become breeders (state M or F) before they could be re-encountered.

During the first year of re-encounter, birds had to be trapped during incubation to be positively identified, so any factors that affected annual nest survival or trapping efficiency could lead to variation in detection probability. To account for this variation, we calculated annual trapping rate (Trap) as the proportion of unmarked breeding adults that were captured and uniquely banded each year (Appendix 2). Unmarked nesting adults were defined as adults that were still unbanded or banded only with chick bands (ChickBand = 1). Because of their importance in describing variation in detection of first-time breeders, we included either ChickBand or ChickBand × Trap in all models of detection probabilities. The product of Chick- Band × Trap was used as an offset because the disadvantage of having chick bands was most important when trapping rates were low, but low trapping rates did not affect detection rates of previously recruited males or females that need only be resighted.

Data analysis.—We used multi-state capture-recapture models (Brownie et al. 1993, Lebreton and Pradel 2002) to estimate apparent survival (φ) and detection probabilities (*p*) of first-year and adult piping plovers, as well as age- and sex-specific transition probabilities (ψ) from pre-breeder to breeder. After first marking, chicks were treated as unobservable until they transitioned to breeders (Spendelow et al. 2002).

We used an information-theoretic approach (Burnham and Anderson 2002) to select appropriate combinations of age, state, and temporal variation on survival, detection and transition to breeder, and to explore how annual, site, and individual covariates affected these parameters. Use of multi-state models required the following assumptions (Spendelow et al. 2002): after accounting for age, state, and covariate effects, 1) every bird had the same probability of survival from period *i* to *i* + 1; 2) every marked bird present in the population at time *i* had the same probability of being recaptured or resighted; 3) every marked pre-breeder at the beginning of sampling period *i* had the same probability of becoming a breeder; 4) marks were not lost and were recorded correctly and 5) the fate of each bird was independent with respect to capture, survival, and transition probabilities. In addition to these standard assumptions, multi-state models further assume: 1) survival from time *i* to *i* + 1 does not depend on state at time *i* + 1 (i.e. survival is conditional on the previous state, not the future state) and 2) all individuals make the transitions at the same time, relative to the start or end of the time interval (Cooch and White 2012). Aside from newly nesting birds that may have been killed before they could be trapped and identified as breeders, the first assumption was presumably met. For the second assumption, most birds were re-encountered during the

beginning of each breeding season, so individuals 'transitioned' from pre-breeder to breeding adult at the beginning of each survival interval.

Because we designated three states in our analysis, our models included nine transition probabilities (note: remaining in same state is a transition probability). However, only three of these transitions were biologically meaningful: remaining a pre-breeder (ψ^{PP}) or transitioning from a pre-breeder to a first-time breeding male (ψ^{PM}) or female (ψ^{PF}). We used a multi-nomial logit link (i.e. MLogit; Cooch and White 2012) to constrain $\psi_a^{PP} + \psi_a^{PM} + \psi_a^{PF} = 1$ for each age class (denoted as 'a' subscript). We also set *p* of state P as 0 (i.e. unobservable). We treated states M and F as absorbing states and fixed $\psi^{MM} + \psi^{FF} = 1$; transitions that were biologically impossible (e.g. transitioning from one sex to the other, ψ^{MF} and ψ^{FM} ; or from a bird that has already bred to one that has not yet bred, ψ^{MP} and ψ^{FP}) were fixed to 0. Because pre-breeders were of unknown sex, we divided model-based estimates of transition probabilities for each sex by the estimated proportion of pre-breeders of that particular sex. For age one, we assumed a 50:50 sex ratio at banding and no differential mortality between pre-breeding males and females, and hence we divided model-based estimates and their standard errors by 0.5. We made similar adjustments for older age classes, but because of sex-specific differences in recruitment at earlier ages, we had to explicitly estimate the sex ratio of remaining pre-breeders at each age class. Assuming no differential mortality prior to breeding, we estimated a sex ratio of $(1 - \psi_1^{PM}):(1 - \psi_1^{PF})$ for age two and $(1 - \psi_1^{PM})(1 - \psi_2^{PM}):(1 - \psi_1^{PF})(1 - \psi_2^{PF})$ for age three pre-breeding individuals (subscripts denote age classes). Hence, the estimated breeding propensity of males at age three was $\psi_3^{PM} /[((1 - \psi_1^{PM})(1$

$- \psi_2^{PM}$))/((1 – ψ_1^{PM}) (1 – ψ_2^{PM}) + (1 – ψ_1^{PF}) (1 – ψ_2^{PF}))]. We estimated standard errors of sex-specific transition probabilities using the delta method (Powell 2007).

Multi-state models were fit using maximum likelihood procedures in Program MARK (White and Burnham 1999) and assessed using Akaike's information criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002). We estimated a variance-inflation factor of $\hat{c} = 0.75$ using Program U-CARE ver. 2.3.2 (Pradel et al. 2005), so we did not adjust for over dispersion (Cooch and White 2012). Multi-state models can have multiple local optima, so we used the simulated annealing (Alt Opt) feature in MARK to verify convergence of top-ranked models.

Model selection.—We varied model structure by state (pre-breeder [state P], male breeder [M], female breeder [F]), age class (1–4; where values are age in years at the end of each interval, except for the oldest age class which includes all individuals of that age or older), time (constant or fully temporal), and the 12 covariates described above. To simplify our modeling approach, we slightly modified a method proposed by Bromaghin et al. (2013) and conducted our modeling in four stages (Appendix 3).

We began model selection with detection probability because we wanted to account for known resighting heterogeneity of chick- versus adult-banded individuals before evaluating survival and transition probabilities. In this first step, survival and transition probabilities were modeled using complex yet biologically reasonable structures: state (= sex) × time × two ages for survival and state (sex) × four ages for recruitment. We included covariates denoting years when individual plovers wore chick bands in all models to correct for known resighting heterogeneity of individuals banded with chick versus adult bands, and we also considered interactions between chick bands

and trapping effort (ChickBand × Trap). Using design matrix constraints in Program MARK, we were able to model ChickBand and ChickBand × Trap using only two additional parameters (Appendix 2). All models with $\Delta AIC_c < 7$ of the top model were carried forward to stage two of model selection.

For stage two, our primary interest was to measure age-specific probability of first breeding, and thus we modeled ψ by varying age classes (one through four-plus years old) as well as sex (i.e. age-specific transition probabilities set equal between sexes or kept as different by default). Because transition data were sparse (surviving individuals transitioned only once), we did not attempt to model temporal variation in ψ. We considered a maximum of four age classes on ψ because all but one bird in our dataset were first observed breeding by age four. Survival probability was kept at its most complex structure (age × state × time) to fully account for any variation that might be better explained by φ. Resighting probability was modeled according to the two structures chosen in stage one. Models with $\Delta AIC_c < 7$ were carried forward to the third stage.

All stage-three models included juvenile versus adult age structure on survival (i.e. two age classes). Preliminary investigation indicated no support for models recognizing three or more age classes on survival, so we did not consider them further. We varied model structure for survival by sex, time and combinations of age, sex and time, as well as annual covariates.

Because birds in state one were unobservable, we had to set their survival rates equal to birds in an observable state (Kendall and Nichols 2002). We therefore set survival probability of state one (pre-breeders) equal to state two (male breeders). We

assumed that pre-breeder survival rates would be more similar to males because females might experience higher costs of reproduction (Nager et al. 2001). Transition probabilities in all stage-three models were fixed to vary by the single top-supported structure selected in stage two; resighting probability was fixed to vary by the two top-supported structures identified in stage one.

When considering annual covariates on φ (Table 1), we began with an intercept-only model with a constant survival structure that varied by state, with chick survival set to follow males after their first year. We then added annual covariates individually to each group (i.e. chicks only, adults only, or both chicks and adults). Covariates that reduced AIC_c relative to the intercept-only model were retained to build 2- and 3-covariate combinations. All survival models with $\Delta AIC_c < 7$ were carried forward to the fourth and final stage.

We used the top-ranked models from the second and third stages as templates for the addition of individual covariates (Table 1) on first-year survival in our final stage. We also added pertinent individual covariates to age one transition probabilities from pre-breeder to breeder. All individual covariates that led to reductions in AIC_c were retained and used to build models containing two or more covariates. The model with the lowest AIC_c after these four steps was considered the top-supported model. All parameter estimates are reported as mean ± standard error (SE) unless otherwise noted.

In a post-hoc investigation of the timing of individual covariate effects on first-year survival, we considered interaction terms between banding age and the individual covariates that were supported in our top model (e.g. a BandAge × Condition interaction could indicate that Condition only affected survival of chicks banded at young ages,

indicating the effect was entirely pre-fledging). Given our results from this analysis, we re-ran all multi-state models using a dataset which excluded chicks that died prior to fledging (n = 376 individuals omitted; 20% of original data set) in order to obtain a more robust first-year survival estimate post-fledging. We were unable to identify chicks uniquely because of batch markings, so we randomly removed individuals (except for those who were seen in subsequent years) from each brood according to the known number of fledglings per brood. The standardized condition covariate was adjusted accordingly and other mean values of individual covariates (e.g. cohort size, banding age) were re-calculated. All models were re-run as described previously using this new data set, except BandAge was excluded due to its irrelevance in describing survival post-fledging. Results from this analysis were compared to those from the original analysis that incorporated interaction terms to assess the influences of individual covariates at affecting first-year survival during the pre- versus post-fledging stages.

RESULTS

We encountered 2955 birds, including newly marked chicks and adults, plus recaptures and resightings of previously marked birds. The number of juveniles and adults banded annually increased over the study period due to increases in population size and improved banding efforts. A total of 165 males and 158 females were banded as chicks and encountered during at least one occasion in a year following their year of hatch; 57 males and 63 females were banded as adults. We also summarized means and standard deviations for individual and annual covariates (Table 1).

The best-supported model of detection probability (Table 2) included an occasion-specific ChickBand effect ($\beta = -3.87 \pm 0.516$) and a combined effect of ChickBand ×

Trap ($\beta = 4.19 \pm 0.994$). For individuals wearing adult bands (ChickBand = 0), mean detection (i.e. resighting) probability was 0.929 ± 0.009 and constant among years and between sexes (Fig. 2). For individuals wearing chick bands (ChickBand = 1), mean detection (i.e. physical capture) probability varied greatly by year (0.35 during 2003 to 0.90 during 2006) as a result of variation in trapping effort (Fig. 2). These results were robust to model structures that included sex-specific variation in detection probabilities ($\Delta AIC_c = 1.01$). We only report results from models without sex-specific differences in detection because the model without the sex effect was more parsimonious.

Including the pre-fledging period, first-year survival was positively related to banding age ($\beta = 0.071 \pm 0.018$, Fig. 3A), cohort size ($\beta = 0.020 \pm 0.009$, Fig. 3B), and body condition ($\beta = 0.711 \pm 0.345$, Fig. 3C); survival was negatively related to standardized hatching date ($\beta = -0.250 \pm 0.079$, Fig. 3D). Standardized hatching date and age at banding were important predictors in all top-supported models (Table 2). We found no support for time variation or annual covariate effects on first-year survival.

When interaction terms (BandAge × StdHDate; BandAge × Condition; BandAge × CohortSize) were added to the top-supported model, the positive effects of body condition and cohort size on first-year survival were primarily due to their effects pre-fledging, rather than post-fledging (Table 3). However, the negative relationship between standardized hatching date and survival was a result of influences on both pre-fledging and post-fledging periods (Table 3). Excluding data where chicks died prior to fledging confirmed these trends; first-year survival was no longer affected by condition or cohort size, but increased with early standardized hatching dates ($\beta = -0.262 \pm 0.083$).

Annual survival of first-year plovers was 0.284 ± 0.019 from mean banding age (9 d old) to the beginning of the next breeding season; however, this included some mortality that occurred between banding and fledging. Using the dataset that excluded chicks that died prior to fledging, a more robust estimate of first-year survival from fledging age was 0.374 ± 0.023.

Adult survival was negatively related to annual abundance of eastern North American merlins during the non-breeding season ($\beta = -0.020 \pm 0.004$, Fig. 4A) as well as annual hurricane counts ($\beta = -0.132 \pm 0.058$, Fig. 4B). Merlins were an important predictor in all top-supported models, and a hurricane effect was supported in 4 of 8 top models (Table 2). Minimum mean spring temperature was a moderately important predictor ($\beta = 0.057 \pm 0.035$) of adult survival; it was supported in the fifth-best model and in 3 of 8 top models (Table 2). Mean adult survival was 0.742 ± 0.022 for males and 0.725 ± 0.024 for females; however, a sex-specific difference in adult survival was not supported by AIC_c.

The probability of transitioning from pre-breeder to breeder varied by sex and age (Table 2). Although condition of chicks at time of banding positively affected the probability of breeding as a one-year-old ($\beta = 1.117 \pm 0.618$), this effect was no longer supported when chicks that died before fledging were censored from the analysis ($\beta = 1.155 \pm 0.725$). Age-specific recruitment probability differed between males and females, with females having a higher probability (0.557 ± 0.066) of breeding during their first year compared to males (0.353 ± 0.052). Of those surviving individuals that did not recruit yet, males had a higher probability of recruiting in either their second (0.693 ± 0.120) or third year (1.000 ± 0.335) when compared to females (0.433 ± 0.121; 0.644 ±

0.183, respectively). Without using a multi-state model to properly account for lower detection probabilities of chick-banded birds, age at first breeding would have been overestimated by ~15% for both males and females (Table 4), with several individuals not detected breeding until their second to fourth breeding attempts.

DISCUSSION

Our estimate of survival (0.374) for post-fledging Great Lakes piping plovers during their first year of life was similar to that of studies that estimated first-year survival in other piping plover populations (Larson et al. 2000, 0.318, Calvert et al. 2006, 0.342 [Gulf of St. Lawrence population segment]). Including pre-fledging mortality had a large effect (Roche et al. 2008), as our estimate of first-year survival was only 0.284 when based on a mean banding age of 9 d. Most population models for piping plovers use counts of fledglings as measures of fecundity, so it is important that measures of first-year survival begin at fledging age, otherwise mortality during the late fledging period will be double-counted. Combining our post-fledging survival estimate with that of Brudney et al. (2013), who measured survival from hatch to fledging age (0.556 ± 0.011), we can achieve a complete understanding of factors affecting first-year survival in this endangered population.

Previous studies have demonstrated lower survival of late-hatching piping plover chicks during the pre-fledging period (Saunders et al. 2012, Brudney et al. 2013, Catlin et al. 2013), and our results indicate that this disadvantage carries over to reduced post-fledging survival. Decreased survival of late-hatching chicks may be a result of deteriorating food abundance (Van Der Jeugd et al. 2009), seasonal increases in predator abundance that lead to greater predation risk for later-hatching chicks (Kruse et al. 2001),

later nesting by less experienced adults who are also less capable parents (Saunders et al. 2012), or reduced investment in late-season young because they have lower reproductive value or higher costs (Daan et al. 1990, Tinbergen and Daan 1990). Excluding the pre-fledging period, we would expect later-hatched chicks to have a shorter period of time in which to grow before the onset of migration and winter (Harris et al. 1992), potentially compromising post-fledging survival.

Including the pre-fledging period, body condition was an important predictor of first-year survival, corroborating results from other species (Schmutz 1993, Naef-Daenzer et al. 2001). Poorer condition has been shown to impair takeoff speed and ascent angle in response to potential predators (Veasey et al. 2000). Although a proportion of variation in body mass is likely heritable, environmental influences are also important (Cooch et al. 1991). Chick growth rates are affected by the availability and quality of food supply, which may vary by year and location (Lepage et al. 1998). Because we found that condition influences survival only during the pre-fledging phase, environmental conditions on the breeding grounds are especially critical. However, if a lighter than average individual survives to fledge, our results indicate that the bird has the potential to recover body condition and thus, overcome this disadvantage post-fledging. This phenomenon has also been demonstrated in sandwich terns (*Sterna sandvicensis*), where chick body condition had strong effects on survival until fledging, but did not influence post-fledging survival (Stienen and Brenninkmeijer 2002). The authors suggested that this lack of a relationship may be due to post-fledging parental provisioning exhibited in this species, buffering juveniles against growth disadvantages

(Stienen and Brenninkmeijer 2002). However, piping plovers do not provide parental care after chicks fledge.

We found that offspring produced at breeding sites with a greater total number of fledglings had greater survival during their first year of life, but this effect was only evident during the pre-fledging period. The presence of similarly-aged conspecifics can promote better development of competitive skills (Spear and Nur 1994) and increase the chance of avoiding predation (Lengyel 2007). Alternatively, sites with a greater number of fledglings may be indicative of higher quality locations with better quality parents or greater prey availability. We suggest two reasons why cohort size was not an important predictor of first-year survival post-fledging: (1) the advantage of fellow fledglings is limited to nesting site only (i.e. no benefit of migrating with more juveniles); or (2) cohort size may be confounded by annual variation in pre-fledging survival.

Our estimates of adult apparent survival (0.742 for males; 0.725 for females) were very similar to that of LeDee et al. (2010), who used a Barker model with wintering ground detections to estimate a true adult survival rate of 0.76 and an apparent survival rate of 0.69 for this same population. Our estimates were also comparable to that of piping plovers in eastern Canada, where adult survival was estimated as 0.73 (Calvert et al. 2006), using a multi-state model that accommodated breeding dispersal among known breeding locations. We found no compelling difference in annual survival between adult males and females, which translates to future life expectancies of 3.35 and 3.12 years, respectively (Brownie et al. 1985). However, survey data suggest that breeding populations have become increasingly male-biased in recent years (Saunders, unpubl.

data), so further analysis is needed to address whether a sex-specific difference in adult survival exists.

Adult survival was negatively correlated with merlin abundance and hurricane frequency in the southeastern United States; however juvenile survival was not affected by either covariate. Previous studies have documented the influence of merlin predation on piping plovers during the breeding season (Murphy et al. 2003, Roche et al. 2010b), and other studies have indicated that merlin predation is a key component of shorebird mortality during the non-breeding season (Page and Whitacre 1975, Johnson and Baldassarre 1988, Drake et al. 2001). Merlin populations in eastern North America have increased almost exponentially in abundance throughout our study (Sauer et al. 2012), and this may be one of the factors contributing to declining survival in this and other piping plover populations (Roche et al. 2010b). Although hurricanes can produce new nesting habitat for Atlantic population piping plovers (Cohen et al. 2009), their impact can also alter foraging habitat, decrease food supply, or directly kill birds (Johnson and Baldassarre 1988, Noel and Chandler 2008).

Females were more likely to mate during their first year than males (56% vs. 35%), and Gratto-Trevor et al. (2010) found a similar pattern for piping plovers in the Great Plains population, with more female plovers breeding as yearlings than males (68% vs. 41%). Males may go unpaired for the duration of their first breeding season or may remain in nonbreeding areas until they are better at competing for breeding territories (Elliott-Smith and Haig 2004). Both explanations would account for the higher probability of female recruitment at age one, as well as the gradual increase in recruitment probability of two- and three-year-old males, as demonstrated in our analysis.

While a lack of breeding opportunities is a likely explanation for deferral of breeding in one-year-old males, it is uncertain what accounts for delayed breeding in females. Available high-quality habitat may be a limiting factor or returning first-year females may have difficulty locating potential mates, given the patchy distribution of unmated males. Applying our estimated survival and recruitment rates to a hypothetical population of 500 fledged female plovers, we estimate that 130 out of 491 potential breeding opportunities (~27%) fail to occur during the first four years of life due to deferred breeding by females that are sexually mature.

CONCLUSIONS

Accurate estimation of demographic parameters and identification of their potential sources of variation are critical for effective conservation management. Our analysis provided more accurate and robust estimates of first-year survival and age-specific recruitment, and helped to identify several important covariates that affect juvenile and adult survival for this population. Early-hatching chicks were more likely to survive their first year, highlighting the need to locate and protect early nests so they hatch successfully. In addition, survival increased with body condition, primarily due to influences prior to fledging, emphasizing the importance of food resources during the brood-rearing stage (Le Fer et al. 2008). Efforts to limit recreational use of important feeding areas, in addition to nesting areas, may ensure access to food sources for growing young (Goldin and Regosin 1998, Elias et al. 2000). To improve adult survival, methods to reduce merlin-induced mortality, especially on the non-breeding grounds, should be explored. It is unclear whether deferred breeding by female piping plovers is due to restraint or constraint (sensu Curio 1983), but up to 27% of the female population fails to

nest in any given year, and any management actions that could decrease the fraction of non-breeders would lead to elevated fecundity. Through these collective actions, managers can further increase recruitment in this federally endangered population.

TABLE 1. Definitions of annual and individual covariates used in multi-state capture-recapture models to estimate apparent survival (φ), detection (*p*), and transition (ψ) probabilities of first-year (FY) and adult (AD) Great Lakes piping plovers during 1993–2012. Abbreviations refer to those used in model notations throughout the text. Parameters are those on which the given covariate was fit during model selection. SD denotes standard deviation.

Covariate abbreviation	Definition	Parameter(s)	Mean ± SD
Annual			
Hurricane	Number of hurricanes impacting southern U.S. Atlantic coast during 15 Aug - 31 Dec	φ_{FY} φ_{AD}	1.2 ± 1.1
MerlinSummer	Estimated merlin abundance in Michigan; measure of predation pressure on breeding grounds	φ_{FY} φ_{AD}	90 ± 13
MerlinWinter	Estimated merlin abundance in eastern North America; measure of predation pressure on non-breeding grounds	φ_{FY} φ_{AD}	119 ± 20
NBTemp	Mean minimum temperature (°C ; 1 March-30 April) based on 3 major non-breeding sites in South Carolina, North Carolina, and Georgia	φ_{FY} φ_{AD}	10.6 ± 2
Trap	Proportion of unmarked and batch-marked nesting adults that were captured and given adult band combinations	p_{male} p_{female}	0.6 ± 0.19
Individual			
ChickBand	Tally of whether bird was wearing chick bands or no bands (1) or whether bird was wearing adult bands (0) on each of 19 encounter occasions	p_{male} p_{female}	-
BandAge	Age (in days) at time of banding	φ_{FY}	9 ± 4
BreedTemp	Mean minimum temperature (°C ; 1 June-31 July) at a given hatch location during year of hatch	φ_{FY}	12.8 ± 3
CohortSize	Total number of fledglings present at a given hatch location	φ_{FY}	10 ± 7
Condition	Residual of $\log_e$-mass of chick at time of banding, regressed on age at banding (days)	φ_{FY} ψ_1^{PM} ψ_1^{PF}	0.0 ± 0.23
HDate	Date of hatch (1 = 1 June)	φ_{FY}	19 June ± 13
StdHDate	Hatching date standardized by mean hatching date of given year of hatch	φ_{FY} ψ_1^{PM} ψ_1^{PF}	0.0 ± 0.9

TABLE 2. Model rankings for top-supported models ($\Delta AIC_c < 7$) used to estimate first-year apparent survival (φ_{FY}; including pre-fledging period), adult apparent survival (φ_{AD}), and age-specific transition probabilities (ψ). Detection probability (p_{AD}) of adults was identical for all top-supported models: ChickBand + (ChickBand × Trap). Detection probability of first-year birds (p_{FY}) was set to 0 in all models. Models were ranked according to differences in Akaike's information criterion (ΔAIC_c) and Akaike weights (w_i). Important covariates included standardized hatching date (StdHDate), age at banding (BandAge), standardized mass at banding (Condition), cohort size (Cohort), average merlin population estimate from Whitefish Point and Hawk Mountain (MerlinWinter), annual hurricane count (Hurricane), minimum mean spring temperature (NBTemp), occasion-specific bands (ChickBand), and annual trapping effort (Trap). A3 refers to 3 age classes. '+' indicates an additive relationship; '×' indicates a multiplicative relationship.

φ_{FY}	φ_{AD}[a]	ψ[b]	ΔAIC_c[c]	Deviance	w_i	k[d]
StdHDate+BandAge+Condition+Cohort	MerlinWinter+Hurriane	(A3×sex)+Condition	0.0000	4296.63	0.46	19
StdHDate+BandAge+Cohort	MerlinWinter+Hurricane	(A3×sex)+Condition	2.2660	4300.92	0.15	18
StdHDate+BandAge+Condition	MerlinWinter+Hurricane	(A3×sex)+Condition	2.3199	4300.98	0.14	18
StdHDate+BandAge+Condition	MerlinWinter+Hurricane	A3×sex	3.6513	4304.34	0.07	17
StdHDate+BandAge+Cohort	MerlinWinter+NBTemp	(A3×sex)+Condition	4.6013	4303.26	0.05	18
StdHDate+BandAge+Condition	MerlinWinter+NBTemp	(A3×sex)+Condition	4.7991	4303.46	0.04	18
StdHDate+BandAge+Condition	MerlinWinter	(A3×sex)+Condition	5.6830	4306.37	0.03	17
StdHDate+BandAge+Condition	MerlinWinter+NBTemp	A3×sex	6.1903	4306.87	0.02	17

[a] φ_{AD} structure refers to separate intercepts and a common slope for males and females (e.g., M+F+MerlinWinter+Hurricane).
[b] Condition was added to ψ_1^{PM} and ψ_1^{PF} only.
[c] AIC_c of top model was 4334.91.
[d] k = Number of parameters.

TABLE 3. Timing of individual covariate effects on first-year apparent survival (φ_{FY}) of Great Lakes piping plovers during 1993–2012. Parameter estimates are from the top-supported multi-state model that included the following interaction terms: BandAge × Condition; BandAge × CohortSize; and BandAge × StdHDate. First-year apparent survival is compared during pre- versus post-fledging stages (i.e., banded at 9 vs. 23 days) according to variation in body condition (Condition), cohort size (CohortSize), and standardized hatching date (StdHDate). Survival estimate differences ($\Delta\varphi_{FY}$) in bold indicate an effect of the given covariate on survival at the given stage and are specified under "Timing".

	BandAge	**φ_{FY}**	**SE**	**$\Delta\varphi_{FY}$**	**Timing**
Condition					
6.4 g heavier at 9 days old[a]	9 days	0.337	0.031	**0.110**	Pre-fledging
5.4 g lighter at 9 days old[b]	9 days	0.228	0.031		
6.4 g heavier at 9 days old	23 days	0.515	0.122	0.006	
5.4 g lighter at 9 days old	23 days	0.509	0.107		
CohortSize					
1 chick	9 days	0.250	0.022	**0.117**	Pre-fledging
25 chicks	9 days	0.367	0.045		
1 chick	23 days	0.504	0.097	0.029	
25 chicks	23 days	0.533	0.139		
StdHDate					
30 May[c]	9 days	0.403	0.043	**0.249**	Pre-fledging
25 July[d]	9 days	0.153	0.035		
30 May	23 days	0.655	0.203	**0.241**	Post-fledging
25 July	23 days	0.414	0.139		

[a]Corresponds to 0.33 when standardized. See Fig. 3C.
[b]Corresponds to -0.40 when standardized. See Fig. 3C.
[c]Corresponds to -2 when standardized. See Fig. 3D.
[d]Corresponds to 3 when standardized. See Fig. 3D.

TABLE 4. Real and apparent distributions of age at first breeding (% of distribution shown in parentheses) for 500 fledgling-aged male and female Great Lakes piping plovers, based on predictions from the top-supported, post-fledging model. Real estimates are model-based predictions that account for uncertainty due to detection of first-time breeders, whereas apparent distributions are what would result from interpreting ages of first encounter as true age of first breeding.

	Male		Female	
Age	**Real**	**Apparent**	**Real**	**Apparent**
1	66 (44%)	48 (36%)	104 (68%)	79 (55%)
2	62 (42%)	56 (42%)	26 (17%)	34 (24%)
3	21 (14%)	25 (18%)	16 (10%)	17 (12%)
4+	0 (0%)	5 (4%)	7 (5%)	13 (9%)
Mean	1.70	1.97	1.47	1.68

FIGURE 1. Resighting probabilities of adult-banded Great Lakes piping plovers (light grey solid trendline) and trapping probabilities of first-time (i.e., chick-banded) male breeders (dark grey dash-dot trendline) and first-time female breeders (black solid trendline) from the best-supported multi-state model. Confidence intervals (95%) are shown with a lighter weight in the same color and style as the corresponding trendline.

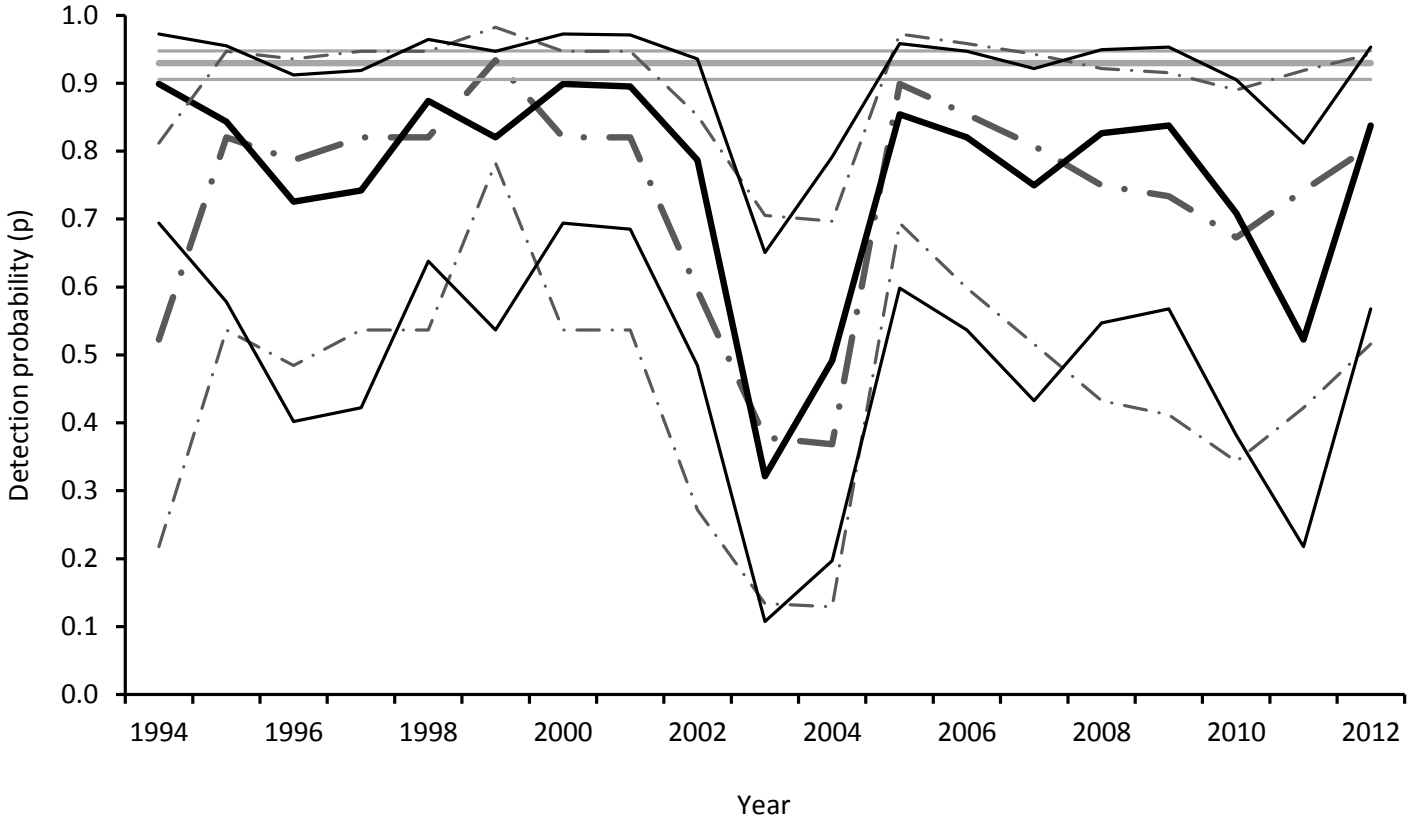


FIGURE 2. Effects of banding age (A), cohort size (B), body condition (C), and standardized hatching date (D) on apparent survival of first-year Great Lakes piping plovers (including pre-fledging period) during 1993-2012. Solid regression lines represent the best-supported multi-state model with all other covariates held constant at mean values. Dotted lines represent 95% prediction intervals calculated using the delta method (Powell 2007). Dashed vertical lines in C and D indicate 0, which is mean body condition and hatching date, respectively. Smaller than average chicks (C; -0.4 = approx. 5.4 g lighter at 9 d old) and early-hatching chicks (D; -2 = approx. 30 May) are represented by negative values; larger than average chicks (0.33 = approx. 6.4 g heavier at 9 d old) and late-hatching chicks (3 = approx. 25 July) are represented by positive values.

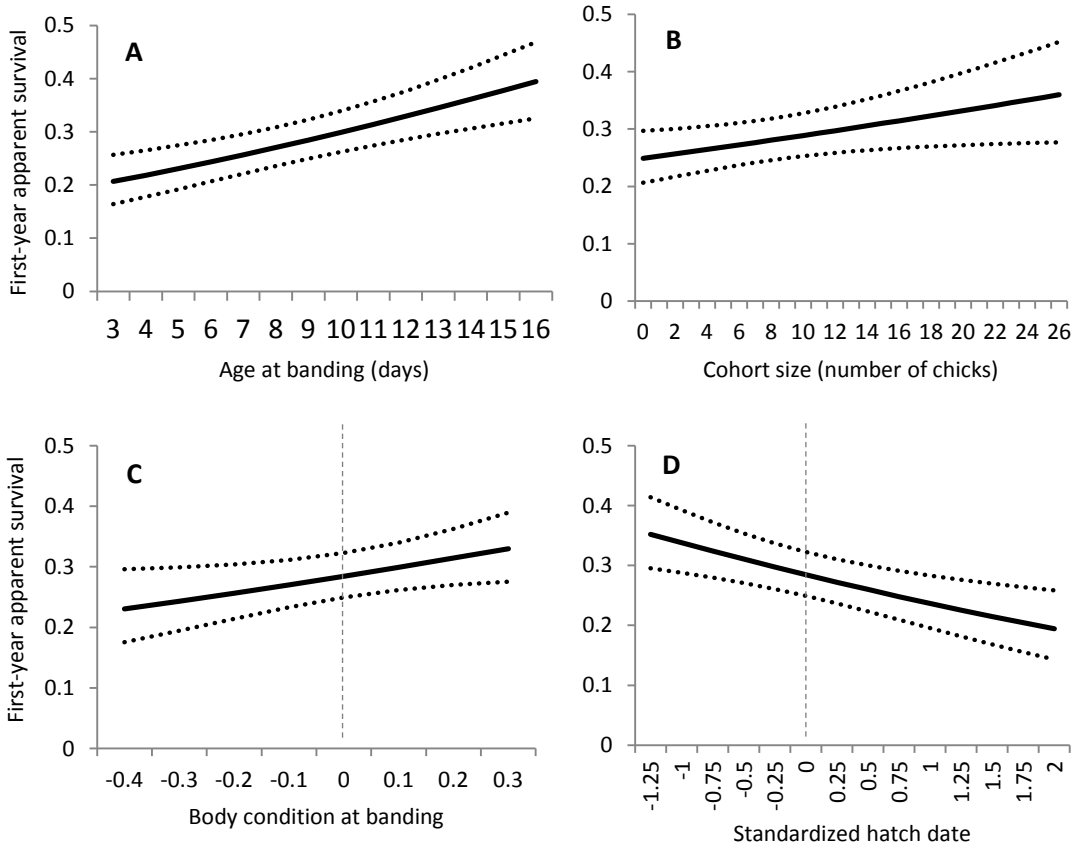
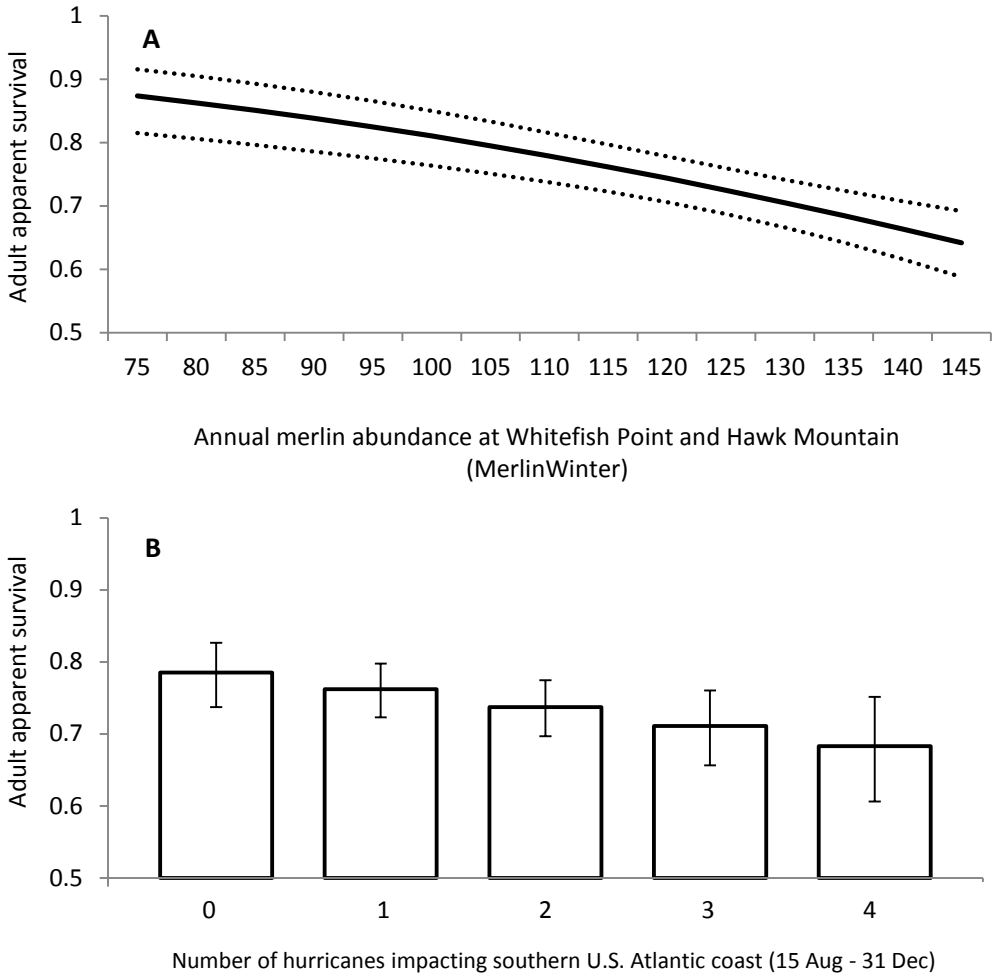


FIGURE 3. Effect of annual merlin abundance at Whitefish Point and Hawk Mountain (A; proxy for wintering merlin abundance) and annual number of hurricanes (during 15 August – 31 December) impacting the southern U.S. Atlantic coast (B) on apparent survival of adult male Great Lakes piping plovers during 1993–2012. Trends are similar for adult female plovers because survival estimates did not differ significantly according to sex. Solid regression line in A represents the best-supported multi-state model with all other covariates held constant at mean values. Dotted lines in A and error bars in B represent 95% prediction intervals calculated using the delta method. Note that *y*-axes begin at $\varphi_{male} = 0.5$.



CHAPTER 4

AUDITORY AND VISUAL THREAT RECOGNITION IN CAPTIVE-REARED GREAT LAKES PIPING PLOVERS (*CHARADRIUS MELODUS*)

CAPTIVE REARING OF endangered species for reintroduction is used to supplement critically small populations because it can potentially increase the rate of recruitment through bypassing the early, high-risk stages in an individual's life history (Crone et al., 2007; Nicoll et al., 2004; Powell and Cuthbert, 1993). Mammalian and avian populations that have increased in size after release of young bred or raised in captivity include the black-footed ferret (*Mustela nigripes*; Miller et al., 1996), peregrine falcon (*Falco peregrinus*; Barclay and Cade, 1983), and Mauritius kestrel (*Falco punctatus*; Jones et al., 2008). In these cases, captive propagation was used as a short-term measure to maintain vulnerable populations until long-term measures could be implemented.

Although some re-introduction programs have been successful, limitations of captive breeding and reintroductions for conserving endangered species are well documented (Maxwell and Jamieson, 1997; Moorhouse et al., 2009; Snyder et al., 1996). Overall, avian rearing and release programs have met with varying degrees of success, but lower survival rates of captive-reared individuals compared to those of their wild-raised counterparts indicate a cost associated with raising or holding an animal in captivity until later release (Aaltonen et al., 2009; Roche et al., 2008; Snyder et al., 1996). Therefore, although captive rearing may increase the survival rate during early life-history stages, the recruitment rate of captive-reared individuals into the breeding population may be comparatively low. Because the purpose of re-introduction programs is undermined if released individuals do not survive to reproduce, it is imperative to refine captive-rearing methods by seeking the reasons for this disparity.

Several hypotheses have been proposed to explain why captive-reared individuals have lower survival rates than those raised in the wild. Alterations in an individual's

surroundings or transportation-induced stress may compromise behavioral integrity (Maxwell and Jamieson, 1997); development of species-typical behavior may require exposure to the species-specific environment, which a captive situation may be unable to replicate (Beck et al., 1994; Swaisgood, 2010); limited exercise space may inhibit proper physiological or morphological development, such as flight muscle development in birds (Hess et al., 2005; Putaala et al., 1997); captive-raised individuals may experience foraging limitations due to unrealistic foraging conditions in captivity or weaker competitive ability post-release (Kleiman, 1989; Kreger et al., 2006); and close, non-aversive interactions with humans during rearing may cause habituation to human presence, potentially decreasing fear during post-release encounters (Hellstedt and Kallio, 2005; Zaccaroni et al., 2007).

A final hypothesis to explain the lower survival rates of captive-reared individuals is deficiency in predator recognition (Griffin et al., 2000; McLean et al., 1999; Shier and Owings, 2006), which was the focus of our study. Defense against predators is an important component of fitness in wild birds, but the first step of defense, predator recognition, is not well understood (Wiebe, 2004). Predation of captive-reared individuals shortly after their release can be a significant source of mortality (Dunham, 1997; Oliver et al., 2008). According to Kreger et al. (2006), lack of predator avoidance has been the greatest behavioral challenge to the success of avian re-introduction programs. Thus, the extent to which predator recognition is learned versus innate is critical information for captive-rearing efforts so that developmental interference and loss of species-specific behavior can be minimized.

Some studies suggest that predator recognition in birds is predominantly an innate response (i.e., no experience required; Galbraith et al., 2007; Veen et al., 2000; Zaccaroni et al., 2007), whereas others emphasize the importance of learning in shaping recognition (Griffin, 2004; Maloney and McLean, 1995; Shier and Owings, 2007). It is reasonable to assume that there should be strong selection pressure on predator-naïve young to recognize predators upon a first encounter (Caro, 2005; Galef and Laland, 2005), but other studies argue that predation risk varies spatially and temporally, necessitating learning to fine-tune responses to local conditions and novel predators or alarm cues (Curio, 1993; Griffin, 2004). Most likely, threat recognition is dictated by both innate and learned components that vary according to the species and environment in which it resides (Caro, 2005). While there is a distinction between the acts of recognition and response, our study specifically examines whether threat recognition is innate in this population because recognition is the critical first step in defense against predators.

Our study explores whether predator recognition in the Great Lakes piping plover (*Charadrius melodus*) is innate or learned by testing vigilant responses of captive-reared chicks to auditory and visual stimuli. Egg salvage and captive rearing of the piping plover began in 1992 at the University of Michigan Biological Station (UMBS) as a recovery method for this federally endangered population (Powell et al., 1997; U.S. Fish and Wildlife Service, 1985); as of 2011, 188 chicks had been released (F. Cuthbert and S. Saunders, unpubl. data). The program is a collaborative effort between USFWS, UMBS, Detroit Zoological Society, >20 Association of Zoos and Aquariums-accredited institutions, and the University of Minnesota. A previous analysis demonstrated 8% apparent survival for captive-reared chicks versus 29% survival for wild-reared chicks

(Roche et al., 2008). Similarly, in the Canadian Great Plains population, resighting rates on the wintering grounds and return rates to the breeding grounds were significantly lower for captive-reared chicks compared to wild-reared chicks (Goossen et al., 2011). The purpose of this study is to determine if captive-reared individuals lack innate recognition of avian predators, potentially explaining their lower survival rate.

METHODS

Focal species and study area.— The piping plover is a small shorebird endemic to North America and restricted to three breeding populations: the Atlantic Coast, Great Plains, and Great Lakes (Haig et al., 2005). The Great Lakes population of piping plovers nests on wide, sparsely vegetated sand and cobble beaches along the shoreline of lakes Michigan, Superior, and Huron in the USA and Canada (U.S. Fish and Wildlife Service, 2003); most of the population occurs in Michigan. Listed as federally endangered in 1986 (U.S. Fish and Wildlife Service, 1985), the Great Lakes population numbered from 17 to 71 known breeding pairs during 1986–2012 (F. Cuthbert and S. Saunders, unpubl. data). Causes of endangerment include heavy recreational use of breeding areas as well as habitat loss due to shoreline development and increased vegetation from invasive species such as phragmites (*Phragmites australis*). To reduce egg predation by mammalian and avian predators, nests are surrounded by wire exclosures as soon as they are discovered (Melvin et al., 1992) and recreational activities are managed where possible to reduce human disturbance in nesting and brood-rearing areas (U.S. Fish and Wildlife Service, 2003). Sources of direct mortality of both chicks and adults include predation by red fox (*Vulpes vulpes*), feral cat (*Felis catus*), domestic dog (*Canis lupus familiaris*), merlin (*Falco columbarius*), American crow (*Corvus brachyrhynchos*), common raven (*Corvus*

corax), and ring-billed gull (*Larus delawarensis*). Although the causes of mortality of released captive-reared birds are unknown, we focus on avian predators as two of the aforementioned avian species (American crow and ring-billed gull) have been documented predating on younger age classes specifically, whereas mammals appear to be less discriminate. As authorized under federal permits, eggs abandoned as a result of mate loss, storm damage, or other forms of disturbance are collected and transported to the captive-rearing facility at UMBS in Pellston, Michigan, USA. When this study was conducted during the 2011 breeding season, 34 eggs were transported to UMBS, 18 hatched, and 16 chicks survived (from seven different clutches) to be reared in captivity (F. Cuthbert and S. Saunders, unpubl. data). Procedures used to hand-rear piping plover chicks are detailed in Powell et al. (1997) and are authorized by USFWS permits.

Data collection.— We used 16 piping plover chicks raised from eggs collected from abandoned nests during May and June 2011. Of these eggs, 56% were abandoned following the disappearance of a nesting adult and 44% were deserted when nests were inundated during storm events. Clutches had been incubated for 4–26 days when they were collected. Each hatched chick was uniquely banded with colored plastic leg bands (Darvic (Avinet; Dryden, NY, USA)) to identify it prior to release and track its post-release survival. On days with amenable weather (temperatures >10 ºC; no or light precipitation), chicks older than 5 days were placed in a 4.6×3.7×1.5-m outdoor exercise pen from 08:00 h to 21:00 h. This structure was comprised of plastic and metal fencing with mesh netting enclosing the top. The pen extended partly into Douglas Lake to provide chicks with experience in a natural shoreline environment, and vegetation was relatively abundant inside the enclosure. All chicks were housed together in the pen, with

a minimum of three chicks and a maximum of 16 chicks in the structure on any given day.

Three separate stimuli treatments were performed: auditory, visual, and auditory plus visual (hereafter audio-visual), to yield a nested 2×7 factorial experimental design: (1) parental alarm (present/absent) by (2) disturbance type (none [white noise], non-predator [three species], predator [three species]). For the auditory treatments, 90-s recordings of 14 different auditory tracks (first three are predators; last three are non-predators) were created in program Audacity 1.3.14-Beta (Audacity Team, 2011) using vocalizations downloaded from The Cornell Laboratory of Ornithology (www.allaboutbirds.org): (1) American crow (AMCR), (2) ring-billed gull (RBGU), (3) merlin (MERL), (4) American robin (*Turdus migratorius*; AMRO), (5) house finch (*Haemorhous mexicanus*; HOFI), (6) house sparrow (*Passer domesticus*; HOSP), (7) American crow + piping plover (PIPL) alarm, (8) ring-billed gull + piping plover alarm, (9) merlin + piping plover alarm, (10) American robin + piping plover alarm, (11) house finch + piping plover alarm, (12) house sparrow + piping plover alarm, (13) piping plover alarm, and (14) white noise (control treatment). The white noise treatment was produced by recording for 90 s in an empty room; when this recording was broadcast, the feedback from the sound system produced a static sound (i.e., white noise). The three predators (American crow, ring-billed gull, merlin) have been documented killing plover chicks; merlins also prey on adults. We tested recognition of the parental alarm call to determine whether chicks were capable of identifying threats indirectly via responses to conspecific cues. Auditory tracks including vocalizations paired with the parental alarm call were included to further test the strength of chick recognition to a conspecific call (i.e.,

whether recognition of a conspecific call alters responses to threatening and non-threatening heterospecific vocalizations). Furthermore, by including the parental alarm call pairings, we were seeking a mechanism by which chicks may learn, which captive-reared chicks would be unable to do without an adult conspecific. Recordings were broadcast from a laptop computer (Dell Inspiron 1570 [Round Rock, TX, USA]) connected to an Insignia 2.1 speaker system (subwoofer and two satellites; NS-PCS21 [Richfield, MN, USA]) from within a blind.

To test visual stimuli, cardboard silhouettes of an American crow (black; 40 cm in length, 85 cm wingspan), ring-billed gull (white; 49 cm in length, 124 cm wingspan), and merlin (brown; 30.5 cm in length, 60 cm wingspan) were attached to a pulley system that was placed approximately 6 m up the nearest tree on the left corner of the pen extending to the opposite right corner of the pen approximately 1.5 m above the ground. To address possible shape effects, a circular piece of brown cardboard with a diameter equal to the average length of a merlin (30.5 cm) was used as a control. These models were paired with their respective auditory threats (i.e., merlin silhouette paired with merlin call and merlin + piping plover alarm call) during the audio-visual treatments. The circle model was paired with white noise, so it was also included in audio-visual treatments.

These treatments were randomized every day of the 39-day study period during June and July 2011. No more than five 90-s trials were conducted consecutively; the average length of time between trials was 12. 5 min (with a minimum of 5 min between trials; Galbraith et al., 2007). These treatment sets were conducted a maximum of three random times a day (with a minimum of 2 h between sets) to mitigate habituation (B. Van Dam, Detroit Zoological Society's Associate Curator of Birds, pers. comm.). We

also sought to control for habituation by including trial date and trial repetition as covariates in our statistical models (see 'Data summary and analyses' for details). Average length of time between testing was 2.5 days. For each trial, one focal bird was chosen at random for observation from within the blind during the 90 s of treatment. For all treatments, the blind used for both observation and vocalization broadcasting was located 1.5 m from the left corner of the pen next to the tree where silhouettes were released. Thus, during audio-visual treatments, both auditory and visual stimuli originated from the same location. Sound emission and silhouette movement began simultaneously to simulate the approach of a live bird as realistically as possible as well as to ensure that chicks initially responded to the combination of auditory and visual stimuli.

On average, each chick was chosen for observation 12.6 ± 0.99 (SE) times; the number of times of observation per chick ranged from 5 (n = 1 chick) to 17 (n = 5 chicks), with 11 (69%) chicks being chosen for 12 or more trials. The same observer recorded behaviors (Table 1) for all trials conducted and was unaware of treatment type beforehand, mitigating potential observer bias. Length of time the behavior occurred was recorded using a stopwatch with a split recording function. Crouching, hiding in vegetation, running, and standing still/looking alert were considered vigilant behaviors, and all others were considered non-vigilant. For all trials, age, date, time of day, and number of chicks in the pen were recorded. Overall, 136 auditory, 20 visual, and 45 audio-visual trials were conducted, for a total of 201 trials. A mean of 12.6 ± 1.4 (SE) trials were conducted per treatment type, with a mean of 8.1 ± 0.73 unique chicks used as focal animals per treatment type (Table 2).

We also collected limited data from vocalization playbacks (11 predator call trials, 6 non-predator call trials) at a wild brood (n = 3 chicks) for comparative purposes. The experimental protocol was similar to that used for auditory treatments of captive-reared chicks: a uniquely banded chick from the brood was chosen and observed for 90 s while a randomly selected recording was broadcast from approximately 3.1 m away under cover of vegetation (i.e., chicks were not responding to investigator presence). Due to the greater distance between observer and wild chicks compared to captive-reared chick trials, binoculars (Pentax Papilio 62216, 8.5 mm×21 mm [Tokyo, Japan]) were used for observation. There was no access to electrical outlets on the beach, so vocalizations were broadcast directly from the laptop without the Insignia speaker system. Thus, testing could occur only when sound conditions were ideal (i.e., no other humans present and no wind). No combined vocalizations with the recorded plover alarm call were used because we wanted to determine during which treatments wild adults would naturally utter alarm calls. A maximum of seven 90-s trials were conducted per day over a 3-day period (chicks were 7, 18, and 24 days old), with a minimum of 15 min between trials. All three chicks were chosen for observation almost equally ($Chick_A$ = 6 times; $Chick_B$ = 6 times; $Chick_C$ = 5 times) over the course of the study.

Data summary and analyses.— Total time spent on vigilant behaviors per trial was calculated and recorded as a proportion of the total trial time. Average percent time spent on vigilant behaviors was considered our response variable in all analyses. We did not transform the response variable because preliminary analyses showed little difference between results using arcsine-transformed and untransformed responses, statistical

models were better fitted using the untransformed variable, and recent work has criticized the arcsine transformation as undesirable for interpretability (Warton and Hui, 2011).

We used two different methods to represent treatment type in our models. The first method classified treatment vocalizations and visuals according to species (i.e., merlin, American robin; hereafter referred to as "species treatment") and the second method classified treatments according to general categories (i.e., predator versus non-predator; hereafter referred to as "general treatment"). Using both classifications of treatment type allowed us to test whether chicks exhibited species-specific responses or simply responded to a general threat. A separate covariate was used to tally whether a given trial included a plover alarm vocalization. The following two *a priori* covariates were included in all statistical models because of their potential importance in affecting daily variation in behavior: trial repetition (i.e., tally of how many times a given chick heard a certain vocalization), and Julian date. Date and trial repetition were included to compensate for possible adjustments in behavior due to learning throughout the course of the study. We added individual chick identity as an *a priori* random effect (Zuur et al., 2009) in all models to account for pseudoreplication of individuals and potential non-independence of trials.

We used linear mixed models (package lme4) in R version 2.12.0 (Bates and Maechler, 2010) to investigate sources of variation in average percent time spent on vigilance during auditory, visual, and audio-visual treatments of captive-reared piping plover chicks. We fitted eight models, which differed according to the inclusion of the following covariates: (1) null model with only random effect of chick identity, (2) parental alarm call alone, (3) species treatment, (4) general treatment, (5) species

treatment with additive parental alarm call, (6) general treatment with additive parental alarm call, (7) species treatment with a species-by-parental alarm call interaction, and (8) general treatment with a general-by-parental alarm call interaction. We fitted models five and six to test whether it is the combination of two treatments that triggers a behavioral response; we fitted models seven and eight to test whether the parental alarm call alters behavioral responses to either the species-specific or general treatment, respectively. Models were ranked based on Akaike's information criterion adjusted for small sample size (AIC_c) and the model with the lowest AIC_c was retained as the top-supported model (Burnham and Anderson, 2002). Comparisons of means and 95% confidence intervals were used to interpret differences in vigilance according to treatment types supported by AIC_c.

RESULTS

During all non-predator auditory treatments, chicks did not crouch, run, or hide; remaining still and alert was the only vigilant behavior observed (Table 3). Frequently, this behavior occurred at the beginning of the trial when chicks responded initially to the sound of a vocalization nearby (63% of non-predator trials); the majority (89%) of individuals resumed their foraging within 15 s. For predator auditory treatments, however, chicks exhibited the range of vigilant and non-vigilant behaviors, with the most time spent remaining still and alert, on average, for all predator types (average of 46–51% of trial time; Table 3). The longest mean period of alertness was exhibited during the parental alarm call (54.8 ± 2.9 s), and chicks spent the least amount of time walking/foraging, on average, during this treatment (5.9 ± 1.1 s; Table 3).

Variation in chick vigilance was better predicted by general predator and non-predator categories compared to species-specific classifications. The best-supported model for percent time spent on vigilance included the general treatment, parental alarm call, and their interaction. The next best model included the species treatment, parental alarm call, and their interaction, but differed by >7 AIC_c (-69.90 and -62.59, respectively; Table 4). Chicks were significantly more vigilant in response to predator stimuli compared to non-predator stimuli and white noise. A 20% increase in vigilance occurred, on average, during non-predator treatments as compared to white noise (95% CI: 8.0–34.2%), while an average increase of 77% in vigilance during predator treatments (95% CI: 65.7–91.1%) compared to white noise was observed (Fig. 1). Vigilance also increased by an average of 56% during predator treatments compared to non-predator treatments (95% CI: 49.8–64.8%; Fig. 1).

During parental alarm call vocalizations, time spent on vigilant behaviors increased by 91% (95% CI: 85.2–98.5%) when compared to white noise. The influence of the parental alarm was further illustrated through a 40% increase (95% CI: 31.8–50.2%) in vigilance when the plover alarm was added to non-predator treatments, and a 12% increase (95% CI: 4.9–19.2%) when added to predator treatments (Fig. 1). Although chicks increased vigilance with the addition of the plover alarm to all treatment types, vigilance was significantly higher during plover + predator treatments compared to those of plover + non-predator (Fig. 1).

Piping plover chicks appeared unable to differentiate between degree of auditory threat; they did not show significant differences in average percent time spent on vigilance among distinct predator calls (95% CIs overlap with exception of the crow call;

Fig. 2). In addition, plovers did not demonstrate species-specific reactions amongst non-predator calls (all 95% CIs overlap; Fig. 2). Likewise, the addition of the plover alarm did not elicit any significant differences among predator and non-predator treatments (Fig. 2). Our top-supported model also indicated that general treatment explained more of the variation in chick vigilance than species-specific treatments, suggesting only a general recognition and response to threats and non-threats. No discernible differences were observed in responses to auditory, visual, and audio-visual stimuli for predator species treatments, with the exception of the crow auditory versus audio-visual treatments (Fig. 3). The full-sensory merlin model (i.e., plover + merlin auditory with merlin visual) was the only full predator treatment to significantly increase vigilance relative to all plover + non-predator auditory treatments (Fig. 3), suggesting a possibly weak species-specific recognition of merlins.

Threat recognition during vocalization playbacks at a wild brood did not reveal a difference between average percent time spent on vigilance (± SE) during all predator vocalizations when compared to captive-reared chicks ($\mu_{captive}$ = 78.3% ± 2.8%; μ_{wild} = 75.4% ± 5.7%). However, wild chicks were less vigilant during all non-predator vocalizations compared to captive-reared individuals ($\mu_{captive}$ = 21.9% ± 3.1%; μ_{wild} = 8.0% ± 6.0%).

DISCUSSION

Our results provide strong evidence that piping plovers innately recognize avian predators. Chicks spent significantly more time on vigilant behaviors during all predator treatments compared to all non-predator treatments and white noise. Although it is unclear what feature of the predators' vocalizations plovers respond to (e.g., structure,

pitch), the concept that predator recognition is innate in birds has a long history in animal behavior, dating back to studies by Lorenz (1939) and Tinbergen (1948). Additional studies have demonstrated innate predator recognition in predator-naïve birds. For example, several species (*Ficedula hypoleuca*, *Taeniopygia guttata*, *Colaptes auratus*) from predator-free islands or raised in captivity have been shown to distinguish between threatening and non-threatening animals in response to the presentation of model predators (Curio, 1975; Lombardi and Curio, 1985; Wiebe, 2004). Investigations of predator recognition in hatchlings are rarer than those of predator-naïve adults, presumably because such studies are logistically difficult to conduct. Of those that have been performed, several demonstrate innate threat recognition in newly hatched or young individuals. For example, studies have shown innate recognition of venomous snakes by naïve, hand-reared green-backed herons (*Butorides striatus*), egrets (*Casmerodiles albus* and *Egretta thula*), and great kiskadees (*Pitangus sulphuratus*); in the case of green-backed herons, the snakes did not occur in the same region as the herons (Caldwell and Rubinoff, 1983; Smith, 1977).

Although the degree to which predator recognition is learned likely varies according to species, we might expect precocial birds to possess innate responses because of their independent nature soon after hatching (Curio, 1993). Unlike altricial species, precocial species leave the nest area within hours of hatching and are more likely to encounter predators, perhaps without a parent nearby. In piping plovers, individuals in a brood may frequently forage independently within the first several days of hatching, often wandering substantial distances (i.e., several hundred m) from their parents

(Haffner et al., 2009). Thus, this type of behavior would favor chicks that are born with an innate ability to recognize potential predators.

While the foundation of threat recognition appears to be innate in piping plovers, individual species recognition may require a learning component. Although plovers are able to differentiate between predator and non-predator stimuli, we did not find any evidence for variations in vigilance within predator or non-predator types. This result suggests that either plovers do not discriminate amongst predator and non-predator species, or such variations in responsiveness are refined through learning from parental or conspecific cues. In this case, learning may be occurring by beginning with a generalized innate recognition of a wide variety of stimuli, and developing into a learned response to a specific set of dangerous objects (Caro, 2005).

Chicks demonstrated the greatest increase in vigilance during the parental alarm call treatment and vigilance also increased whenever a treatment was paired with a parental alarm call, regardless of whether it was a predator or non-predator stimulus. Therefore, innate recognition of the conspecific alarm call appears to be the most defined in plovers, as compared to responses to predator calls alone. This observation confirms behaviors documented in other avian species, such as in captive-reared kaki (*Himantopus novaezelandiae*), where chicks innately recognized conspecific alarm calls (Galbraith et al., 2007). Additionally, wild mallard ducklings (*Anas platyrhynchos*) froze upon initial exposure to maternal alarm calls (Miller et al., 1990) and nestlings of three altricial species ceased begging only in response to conspecific alarm calls, even when individuals were raised by parents of another species (Davies et al., 2004). Increased vigilance in response to conspecific alarm calls can provide an evolutionary advantage

because predator communities vary throughout plover breeding and wintering ranges, so recognition of plover alarm calls that can be associated with novel predators is more beneficial than simply recognizing vocalizations of a limited group of predators. It is important to note, however, that this strong innate recognition of parental alarm calls, combined with extensive time spent with at least one parent prior to fledging (approx. 20 days; Cairns, 1982), suggests a learning component that is perhaps absent in captive-reared individuals. The exact behaviors wild chicks may learn during the pre-fledging period remains unknown, but it is likely that chicks benefit from learning to associate danger with species they may not inherently have perceived as such without the benefit of parental recognition.

We found no discernible differences in responses to auditory, visual, and audio-visual stimuli for predator species treatments, with the exception of crow auditory versus audio-visual treatments. These results indicate that chicks are relatively equally responsive to auditory and visual stimuli. Prey animals commonly use several cues to recognize danger that include sight, sound, and odor of predators, or a combination of these sensory modalities (Caro, 2005). Consequently, it is reasonable to expect chicks to respond similarly to both auditory and visual stimuli as individuals should be able to recognize such cues independently or in combination to adequately avoid danger.

Circumstantial observations of captive chick threat recognition post-release revealed similar responses to avian predators as seen during our trials. Furthermore, a preliminary examination of wild chicks showed that the average percent time spent on vigilance in response to predator vocalizations was very similar to that of captive-reared chicks. In contrast, when exposed to the calls of non-predators, there was some evidence

that wild chicks were relatively less vigilant than captive-reared chicks. Despite the small sample size of wild observations, there appears to be a decreased response to non-predators, perhaps due to learning from parents that such vocalizations are not a threat. Indeed, during playback to the wild brood, parents uttered an alarm vocalization only when predator calls were played. Although captive-reared chicks continued to respond effectively to avian predators post-release, observations of seven individuals at two release sites indicated a decreased timidity around humans (A. Van Zoeren and S. Saunders, pers. obs.). This may be a result of the rearing protocol, as zookeepers are not required to wear costumes during handling. Thus, without proper human avoidance behaviors, captive-reared birds could be dying due to human negligence, closer proximity to dogs, or residing on populated beaches that can pose risks to their safety.

There are other issues with captive rearing that may cause decreased fitness upon release into the wild. Different recognition cues and/or escape responses to terrestrial mammalian predators (e.g., red fox, feral cat) may not be innate (Aaltonen et al., 2009). Decreased stamina from lack of exercise in captivity may inhibit flight muscle development, potentially impacting the ability of released young to complete the fall migration (Hess et al., 2005). Preliminary investigations comparing morphological development in wild and captive-reared piping plovers indicate a significantly smaller keel score at fledging age for captive-reared birds, potentially supporting this hypothesis (S. Saunders, unpubl. data). Future work exploring responses to mammalian predators as well as captivity-induced morphological impacts is necessary to either reject or confirm these hypotheses.

CONCLUSIONS

Our results indicate that captive-reared piping plovers innately recognize threats and parental alarm calls. Therefore, captivity does not appear to influence the ability of chicks to recognize the potential danger posed by avian predators, and it is an unlikely explanation for lower apparent survival of captive-reared piping plovers. However, other behavioral responses to predators may need to be learned. The skills of performing appropriate evasive flight tactics or seeking adequate protective cover, for example, are the next steps in the suite of anti-predator behaviors and may only be learned from conspecifics during the pre-fledging period (Cresswell, 1993; Pomeroy, 2006). The results of this study can be directly applied to improving captive rearing of piping plovers. Because captive-reared chicks do not appear to differentiate between predator species, initiating predator-avoidance training to further enhance vigilance to currently severe threats (e.g., merlin) or novel predators may improve survival (van Heezik et al., 1999). Raising captive chicks in the presence of an adult may allow them to learn certain behaviors that are only acquired during the pre-fledging period in the wild; several unreleasable adults are located in zoos and could be adult models. Reintroduction measures will become increasingly important in the future when more species become locally extinct, but are still produced in captivity. Thus, it is imperative to refine rearing methods to ensure maximum success in augmenting critically endangered populations.

TABLE 1. Ethogram of behaviors recorded during 90-s focal-individual observations of 16 captive-reared Great Lakes piping plover chicks during threat recognition trials.

Behavior	**Definition**
Crouching	Chick suddenly lowers its body to the ground and remains low for at least two seconds
Running	Chick performs a fast-paced movement that is not in obvious pursuit of prey
Standing still and alert	Chick noticeably raises head and looks skyward or around while remaining stationary
Hiding	Specific act of moving from an open space to a vegetated space (preceded by running) and remaining in the vegetation for at least two seconds
Sleeping	Chick sits with eyes closed, apparently unresponsive to visual and auditory stimuli
Walking/foraging	Chick moves slowly and sedately with frequent pauses to peck at the ground

TABLE 2. Stimuli type, number of trials, and number of unique focal chicks used for observation according to treatment type for threat recognition trials of captive-reared Great Lakes piping plovers.

Treatment	**Stimuli type**[a]	**Number of trials**	**Number of unique chicks**
Circle	V	5	3
Crow	A, V & AV	23	12
Crow + Alarm	A & AV	17	11
Finch	A	10	8
Finch + Alarm	A	10	8
Gull	A, V & AV	22	13
Gull +Alarm	A & AV	13	10
Merlin	A, V & AV	18	12
Merlin + Alarm	A & AV	19	9
Plover alarm	A	10	8
Robin	A	10	8
Robin + Alarm	A	10	8
Sparrow	A	7	5
Sparrow + Alarm	A	8	5
White noise	A	10	6
White noise + circle	AV	9	5

[a]A=auditory treatment; V=visual treatment; AV=audio-visual treatment

TABLE 3. Mean time (s) spent on vigilant and non-vigilant behaviors during 201 90-s predator (AMCR, RBGU, MERL), non-predator (HOFI, AMRO, HOSP), parental alarm call (PIPL), and white noise trials of captive-reared Great Lakes piping plovers. ± 1 standard error (SE) is shown. "0" denotes absence of given behavior during treatment.

	Behavior					
	Vigilant				*Non-vigilant*	
Treatment[a]	**Crouch**	**Hide**	**Run**	**Still/Alert**	**Sleep**	**Walk/Forage**
PIPL	3.1 ± 0.9	11.8 ± 2.5	11.1 ± 1.7	54.8 ± 2.9	0	5.9 ± 1.1
AMCR	1.4 ± 0.5	0	11.9 ± 3.5	41.8 ± 3.4	0.9 ± 0.4	30.4 ± 4.1
RBGU	0.8 ± 0.2	4.2 ± 1.3	21.4 ± 2.3	45.0 ± 3.5	0	16.9 ± 4.1
MERL	0	13.4 ± 2.4	11.3 ± 2.0	46.2 ± 4.2	0	13.0 ± 1.6
HOFI	0	0	0	13.2 ± 1.6	9.8 ± 3.2	64.8 ± 3.6
AMRO	0	0	0	11.6 ± 1.5	2.1 ± 0.9	72.8 ± 2.2
HOSP	0	0	0	10.1 ± 1.9	5.8 ± 2.1	65.6 ± 3.9
White noise	0	0	0	1.4 ± 0.7	8.5 ± 3.7	76.6 ± 3.8

[a]PIPL=piping plover; AMCR=American crow; RBGU=ring-billed gull; MERL=merlin; HOFI=house finch; AMRO=American robin; HOSP= house sparrow; White noise=white noise.

TABLE 4. Model rankings for *a priori* models used to estimate vigilance for captive-reared Great Lakes piping plovers. Models were ranked according to differences in Akaike's Information Criterion adjusted for small sample size (ΔAIC_c) and Akaike weights (w_i). Covariates included general treatment (predator vs. non-predator; General), parental alarm call (Alarm), species-specific treatment (Species) and interaction terms (General × Alarm; Species × Alarm).

Model[a]	**ΔAIC_c**[b]	**Deviance**	**Parameters (*k*)**	**Model weight (w_i)**
General + Alarm + General × Alarm	0.00	-90.48	7	0.97
Species + Alarm + Species × Alarm	7.31	-101.20	7	0.03
Species + Alarm	32.01	-66.32	6	1.09E-07
General + Alarm	61.93	-24.40	6	3.48E-14
Species	76.80	-19.41	5	2.05E-17
General	128.86	44.65	5	1.02E-28
Alarm	185.71	103.50	5	4.60E-41
Null model	224.59	144.50	4	1.66E-49

[a]All models (including Null model) contained an intercept term, chick identity as a random effect on the intercept, trial date, and tally of trial repetition (see Methods section for details). Null model had *k*=4 parameters.
[b]AIC_c of top model = -69.90.

FIGURE 1. Effect of general treatment (Treatment) with and without parental alarm call on average percent time spent on vigilance in captive-reared piping plover chicks (*n* = 16). PIPL alarm = plover alarm call (auditory); predator = predator treatments (auditory, visual, audio-visual); PIPL + predator = plover + predator treatments (auditory, audio-visual); non-predator = non-predator treatments (auditory, visual (circle), audio-visual (white noise and circle)); PIPL + non-predator = plover + non-predator treatments (auditory); white noise = white noise treatment (auditory). Error bars represent 95% CI.

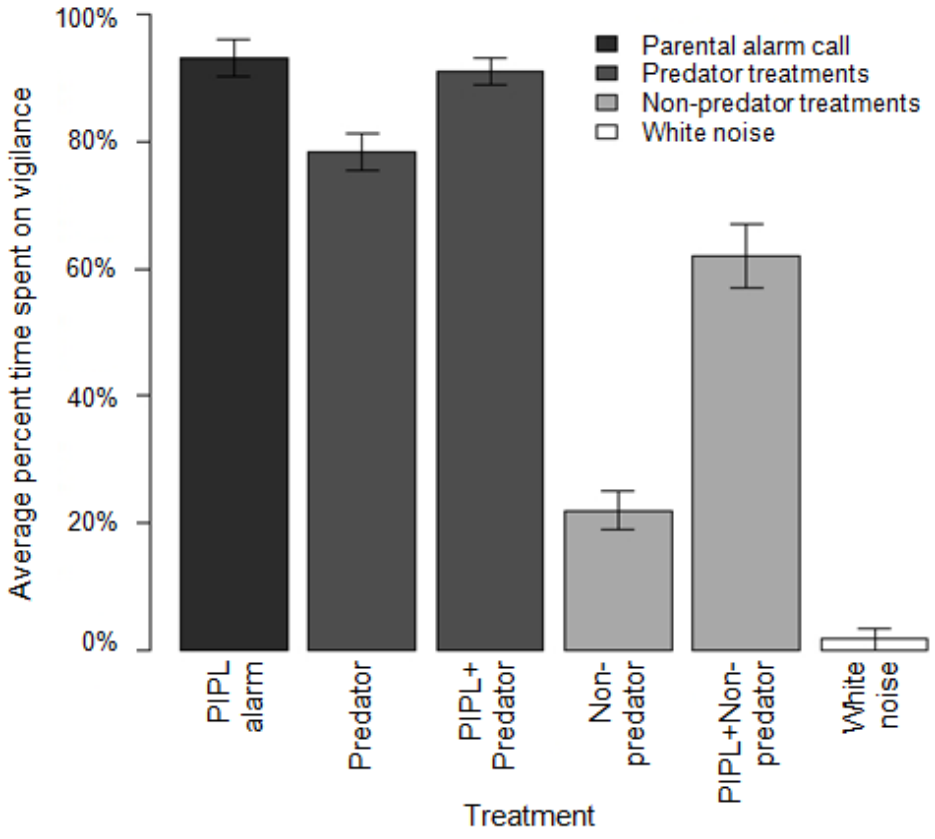


FIGURE 2. Effect of species treatment with and without parental alarm call on average percent time spent on vigilance in captive-reared piping plovers. Error bars represent 95% CI.

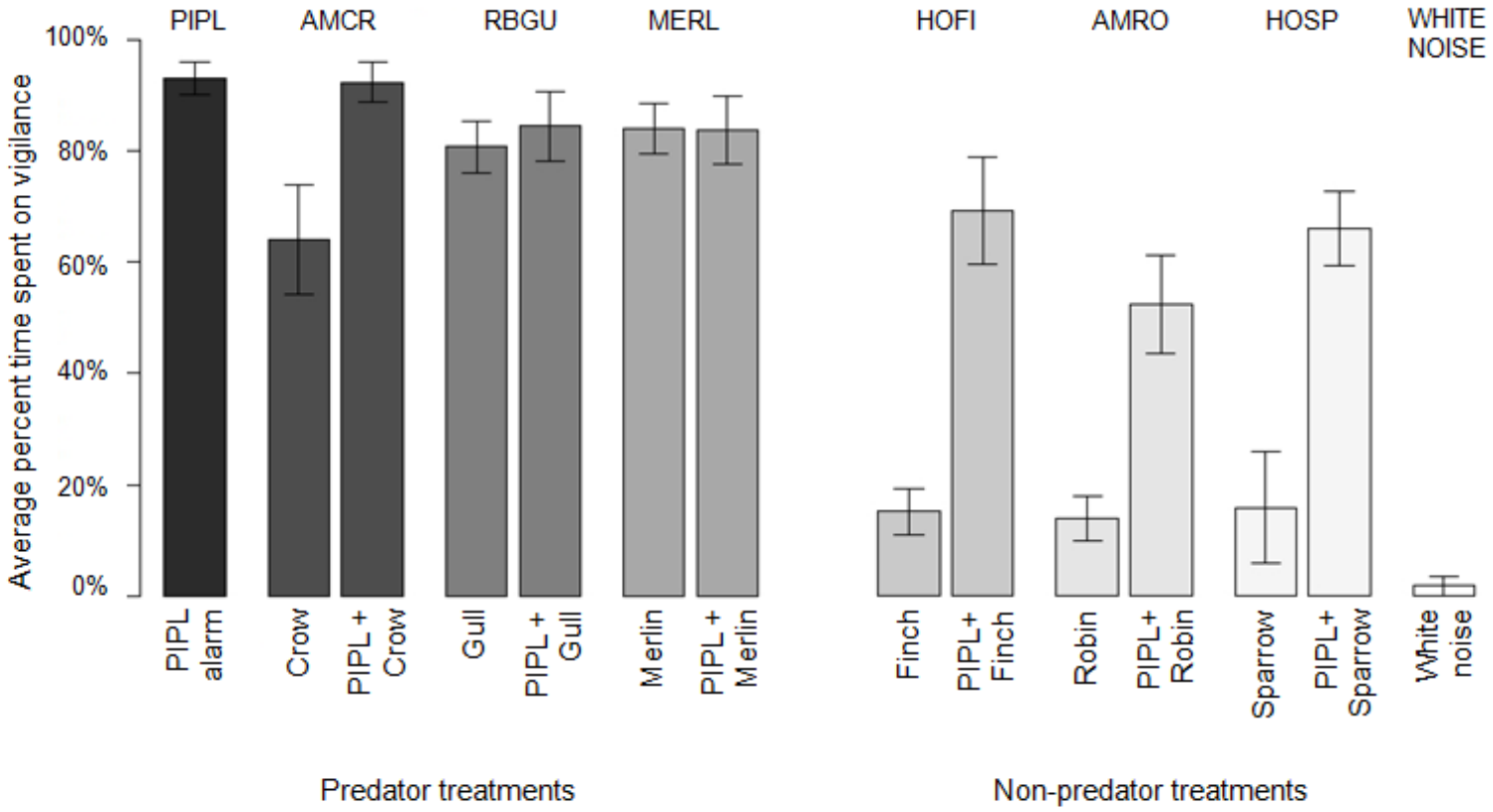
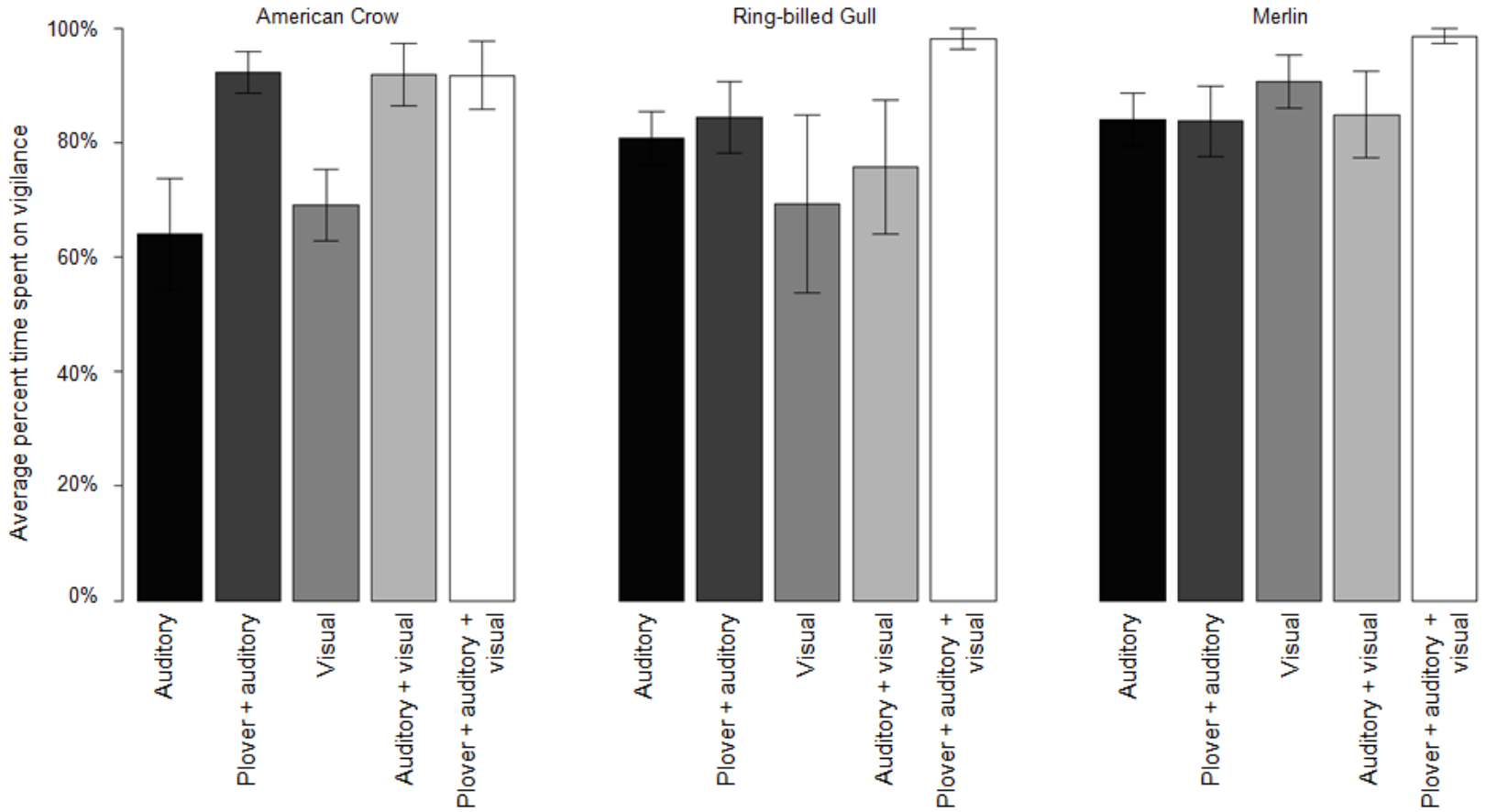


FIGURE 3. Effect of predator treatment type (auditory, visual, audio-visual) on average percent time spent on vigilance in captive-reared piping plovers. Error bars represent 95% CI.



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APPENDIX 1: SUMMARY STATISTICS FOR GREAT LAKES PIPING PLOVER PEDIGREES

TABLE A1. Summary statistics for Great Lakes piping plover pedigrees used to estimate heritabilities of chick body mass (CBM), natal dispersal distance (NDD), and female timing of breeding (TOB). Statistics produced by pedigreeStats function in the R package 'pedantics' (Morrissey and Wilson, 2010).

Statistic	CBM	NDD	TOB
Number of records	2420	405	241
Number of individuals with unknown parents	125	58	40
Number of maternities	2272	326	178
Number of paternities	2269	322	186
Avg. number of generations/Max. number of generations	4/11	3/10	3/9
Mean relatedness	0.024	0.028	0.032
Number of full sib relationships	6535	233	80
Number of maternal sibs/half sibs	15414/8879	486/253	173/93
Number of paternal sibs/half sibs	16321/9786	462/229	162/82
Percent of individuals with non-zero coefficient of inbreeding	28%	20%	17%

APPENDIX 2: MODELING DETECTION PROBABILITIES OF INDIVIDUALS WITH CHICK BANDS

Individuals wearing chick bands could not be positively identified through resighting and had to be physically captured during nesting to achieve positive identification. Therefore, chick-banded plovers had zero probability of being detected prior to transition from non-breeder to breeder, and after they transitioned to become breeders they had lower detection probabilities than birds marked with adult color-band combinations, which could simply be observed with spotting scopes. We assigned each individual a series of 19 occasion-specific covariates (CB94, CB95, … CB12) that indicated years when an individual was wearing chick bands (e.g., CB95 = 1 means an individual wore chick bands in 1995) versus adult bands (CB95 = 0). For example, a chick first marked in 1994 and recaptured as a breeding female and banded with adult bands in 1998 and seen again in 1999, 2000, 2002, 2003 and 2004 would have the following capture history:

01000333033300000000

and the following 19 occasion specific covariates (covariates begin in year 2 since individuals are not resighted in year 1):

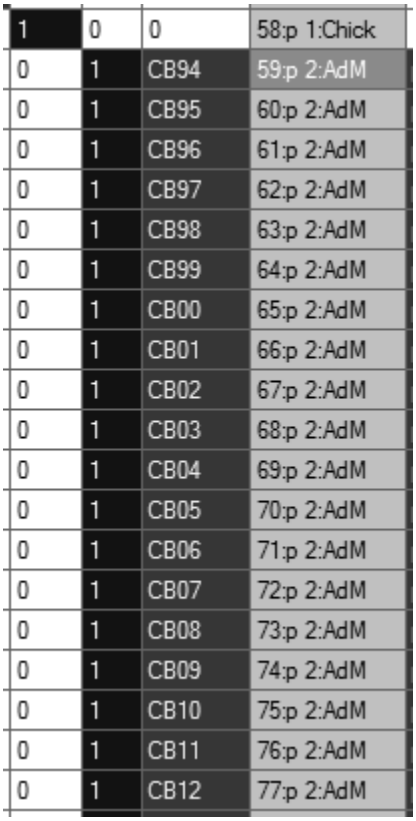
CB94	CB95	CB96	CB97	CB98	CB99	CB00	CB01	CB02	CB03	CB04	CB05	CB06	CB07	CB08	CB09	CB10	CB11	CB12
1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Note that individual covariates are specified as 1 from the year of first marking as a chick up to and **including** the year when individuals were first nest trapped as an adult. These individual covariates allowed us to estimate each individual's (*i*) encounter probability during each year (*j*) by estimating an offset from the detection probability for adult banded birds:

$$\text{logit}(p_{ij}) = \beta_0 + \beta_1 * CB_{ij}$$

Note that when CB = 0, β_0 estimates detection of color-banded adults (year effects could be included with j-2 additional parameters). The design matrix coding for this model in Program MARK would look like Figure A1 (note that even though this model does not estimate year-specific detection probabilities, that each year is included as a separate row to accommodate the year-specific covariates).

FIGURE A1. Design matrix in Program MARK including the CB covariate used to designate whether an individual was wearing chick bands or adult bands.



1	0	0	58:p 1:Chick
0	1	CB94	59:p 2:AdM
0	1	CB95	60:p 2:AdM
0	1	CB96	61:p 2:AdM
0	1	CB97	62:p 2:AdM
0	1	CB98	63:p 2:AdM
0	1	CB99	64:p 2:AdM
0	1	CB00	65:p 2:AdM
0	1	CB01	66:p 2:AdM
0	1	CB02	67:p 2:AdM
0	1	CB03	68:p 2:AdM
0	1	CB04	69:p 2:AdM
0	1	CB05	70:p 2:AdM
0	1	CB06	71:p 2:AdM
0	1	CB07	72:p 2:AdM
0	1	CB08	73:p 2:AdM
0	1	CB09	74:p 2:AdM
0	1	CB10	75:p 2:AdM
0	1	CB11	76:p 2:AdM
0	1	CB12	77:p 2:AdM

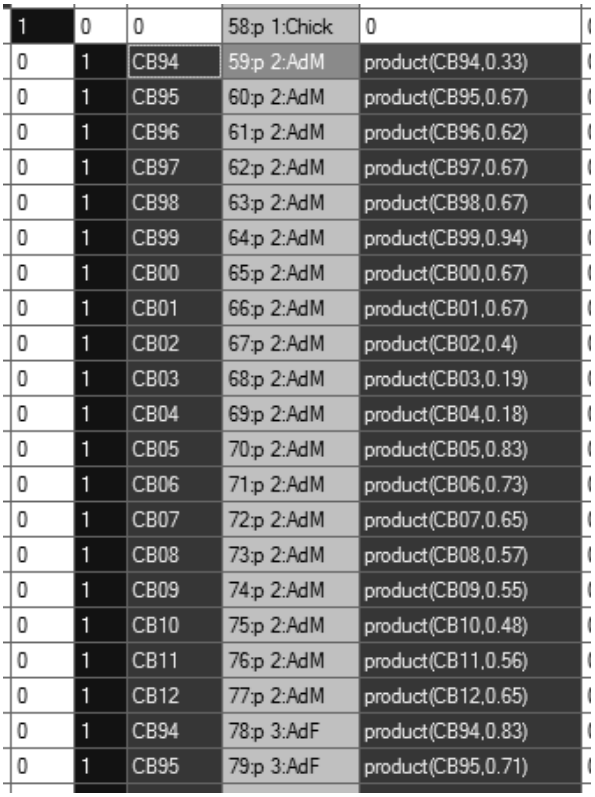
Annual variation in the detection of breeding adults marked only with chick bands is a function of annual trapping success, defined as the proportion of unmarked or partially marked individuals that are successfully nest-trapped and banded with full complements

of color-bands (Table A2). Failure to trap and remark individuals can occur for a number of reasons (i.e., nests fail before trapping can occur, individuals are trap shy and will not enter traps, or logistic difficulties precluded capture attempts) and the variable for trapping success (Trap) accounts for all three potential sources of trapping failure. We summarized trapping success separately for males and females by tallying the total number of unmarked or partially marked individuals that were observed nesting during each field season, and calculating the proportion of these individuals that were captured and uniquely banded during each year, 1994-2012. We included unmarked individuals (~24% of the total) because we had no reason to suppose that their capture probabilities were different from birds wearing only chick bands, and they increased the sample size for estimating trapping success, especially in early years. We tallied results separately by sex in case there were gender differences in trapping success, but aside from considerable annual variability owing to small sample sizes, trapping success did not differ by sex. We considered models using either sex specific trapping rates (antepenultimate and penultimate columns) or pooled trapping rates (last column), and created an additional annual covariate that applied only to birds wearing chick bands by modeling the interaction of CB × Trap (when birds had adult band combinations with CB = 0, this product was also equal to zero). Design matrix coding of this interaction effect is illustrated for males and the first 2 (out of 19) years of females in Figure A2.

TABLE A2. Annual trapping success of adult male and female Great Lakes piping plovers during 1994-2012. 'Both' refers to both sexes combined.

	Total unmarked or chick bands			Total newly banded			Annual trapping rate		
YEAR	**Males**	**Females**	**Both**	**Males**	**Females**	**Both**	**Males**	**Females**	**Both**
1994	6	6	12	2	5	7	0.33	0.83	0.58
1995	9	7	16	6	5	11	0.67	0.71	0.69
1996	13	13	26	8	7	15	0.62	0.54	0.58
1997	9	9	18	6	5	11	0.67	0.56	0.61
1998	12	13	25	8	10	18	0.67	0.77	0.72
1999	16	21	37	15	14	29	0.94	0.67	0.78
2000	9	12	21	6	10	16	0.67	0.83	0.76
2001	18	22	40	12	18	30	0.67	0.82	0.75
2002	25	21	46	10	13	23	0.40	0.62	0.50
2003	21	16	37	4	2	6	0.19	0.13	0.16
2004	22	30	52	4	9	13	0.18	0.30	0.25
2005	35	41	76	29	30	59	0.83	0.73	0.78
2006	26	24	50	19	16	35	0.73	0.67	0.70
2007	31	28	59	20	16	36	0.65	0.57	0.61
2008	28	28	56	16	19	35	0.57	0.68	0.63
2009	42	30	72	23	21	44	0.55	0.70	0.61
2010	25	21	46	12	11	23	0.48	0.52	0.50
2011	18	21	39	10	7	17	0.56	0.33	0.44
2012	23	30	53	15	21	36	0.65	0.70	0.68
Average	**20.4**	**20.7**	**41.1**	**11.8**	**12.6**	**24.4**	**0.58**	**0.62**	**0.60**

FIGURE A2. Design matrix in Program MARK illustrating interaction effect of individuals wearing chick bands (CB) and annual trapping rate.



1	0	0	58:p 1:Chick	0
0	1	CB94	59:p 2:AdM	product(CB94,0.33)
0	1	CB95	60:p 2:AdM	product(CB95,0.67)
0	1	CB96	61:p 2:AdM	product(CB96,0.62)
0	1	CB97	62:p 2:AdM	product(CB97,0.67)
0	1	CB98	63:p 2:AdM	product(CB98,0.67)
0	1	CB99	64:p 2:AdM	product(CB99,0.94)
0	1	CB00	65:p 2:AdM	product(CB00,0.67)
0	1	CB01	66:p 2:AdM	product(CB01,0.67)
0	1	CB02	67:p 2:AdM	product(CB02,0.4)
0	1	CB03	68:p 2:AdM	product(CB03,0.19)
0	1	CB04	69:p 2:AdM	product(CB04,0.18)
0	1	CB05	70:p 2:AdM	product(CB05,0.83)
0	1	CB06	71:p 2:AdM	product(CB06,0.73)
0	1	CB07	72:p 2:AdM	product(CB07,0.65)
0	1	CB08	73:p 2:AdM	product(CB08,0.57)
0	1	CB09	74:p 2:AdM	product(CB09,0.55)
0	1	CB10	75:p 2:AdM	product(CB10,0.48)
0	1	CB11	76:p 2:AdM	product(CB11,0.56)
0	1	CB12	77:p 2:AdM	product(CB12,0.65)
0	1	CB94	78:p 3:AdF	product(CB94,0.83)
0	1	CB95	79:p 3:AdF	product(CB95,0.71)

APPENDIX 3: MODELING STEPS AND RANKINGS FOR MULTI-STATE CAPTURE-RECAPTURE MODELS

TABLE A3. Sequential modeling steps and AIC_c-based model rankings for estimates of first-year (FY) apparent survival, adult (M, F) apparent survival, detection probability of adults, and age-specific transition probabilities of piping plovers during 1993-2012.

Model[a]	**ΔAIC_c**	**Deviance**	***k***
Stage 1: modeling resighting probability			
p(FY = 0, sex × ChickBand × [ChickBand × Trap])	110.3180	4308.11	67
p(FY = 0, ChickBand + [ChickBand × Trap])	109.2620	4313.04	64
Stage 2: modeling probability of first-breeding[b]			
ψ(sex + A2)	109.2620	4313.04	64
ψ(sex + A4)	102.2716	4302.81	64
ψ(sex + A3)	98.9960	4302.77	64
ψ(sex × A2)	92.2416	4296.01	64
ψ(sex × A4)	89.5173	4284.88	68
ψ(sex × A3)	85.5793	4285.15	66
Stage 3a: modeling survival probability			
φ(FY × t, M × t, F × t)	85.5793	4285.15	64
φ(FY × t, sex + t)	64.8657	4291.63	51
φ (FY + t, M + t, F + t)	63.6726	4333.79	30
φ (A2 + t [FY = M = F])	61.9760	4334.14	29
φ (A2 × t [FY = M = F])	61.5615	4296.63	47
φ (FY, M, F)	60.8601	4267.61	12
φ (× t [FY = M = F])	59.5490	4333.76	28
φ (A2 [FY = M = F])	50.7348	4359.51	11
Stage 3b: adding annual covariates to φ			
φ (FY + BreedTemp, M + F + MerlinEast)	42.4329	4349.18	14

φ (FY,M + F + MerlinEast)	42.0601	4350.84	13
φ (FY + BreedTemp, M + F +MerlinTemp + NBTemp)	41.6888	4346.42	15
φ (FY, M + F + MerlinEast + NBTemp)	41.3412	4348.09	14
φ (FY + BreedTemp, M + F + MerlinEast + Hurricane)	39.6384	4344.37	15
φ (FY, M + F + MerlinEast + Hurricane)	39.1927	4345.95	14
Stage 4: adding individual covariates to φ_{FY}			
φ (FY + Condition, M + F + MerlinEast +Hurricane)[c]	33.9686	4338.70	15
φ (FY + Cohort)	30.8583	4335.91	15
φ (FY + HDate)	25.4429	4330.17	15
φ (FY + StandardHD)	25.1980	4329.93	15
φ (FY + HDate + Cohort)	21.3368	4324.04	16
φ (FY + BandAge)	20.9184	4325.65	15
φ (FY + StandardHD + Cohort)	20.5615	4323.27	16
φ (FY + HDate + Condition)	19.8426	4322.55	16
φ (FY + StandardHD + Condition)	19.2515	4321.96	16
φ (FY + Cohort + BandAge)	15.4167	4318.12	16
φ (FY + Condition + BandAge)	14.7977	4317.51	16
φ (FY + StandardHD + BandAge)	11.2974	4314.00	16
φ (FY + StandardHD + BandAge)	10.4223	4313.13	16
φ (FY + StandardHD + BandAge + Cohort)	7.5852	4308.27	17
φ (FY + StandardHD + BandAge + Condition)	3.6513	4304.33	17
φ (FY + StandardHD + BandAge + Condition + Cohort)	1.3574	4300.01	18
Stage 4b: adding individual covariates to ψ_1^{12} and ψ_1^{13} [d]			
ψ(sex × A3 + StandardHD)	3.2782	4299.91	19
ψ(sex × A3 + Condition)	0.0000	4296.63	19

[a]Refer to Table 1 for covariate abbreviations. + indicates an additive relationship; × indicates a multiplicative relationship.
[b]A2, A3, A4 refer to number of age classes (e.g., 2, 3, 4).
[c]Remainder of Stage 4 models all included an effect of MerlinEast and Hurricane on male and female apparent survival.
[d]Individual covariates added to age one transition probabilities from pre-breeder to breeder.